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PLAGUE IN AFRICA FROM 1935 TO 1949
A Survey of Wild Rodents in African Territories

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SYNOPSIS

The history of plague in Africa during the period 1935-49 is reviewed. Much of the information derives from a questionnaire sent to all African territories in 1950. The annual incidence of plague in Africa declined, particularly from 1946 onwards. In 1949, under 400 cases were reported, as compared with over 6,000 in 1935. By the end of 1949, plague was still active in the Belgian Congo, Kenya and Tanganyika, Madagascar, and southern Africa. No cases were reported from Egypt, Tunisia, Algeria, Morocco, Senegal, or Uganda during 1949. A comparison of the seasonal incidence of plague with prevailing atmospheric conditions (temperature and rainfall) in African territories shows that human plague is more frequent in warm moist weather—60°-80°F (15°-27°C)—than in hot dry, or cold, weather—over 80°F (27°C) or under 60°F (15°C). The highlands of equatorial Africa and of Madagascar appear to provide the optimum environment for the persistence of plague on the domestic (murine) plane and the high-veld and Kalahari of southern Africa on the sylvatic plane. The rat (*Rattus rattus*) and the multimammate mouse (*R. (Mastomys) natalensis*) and their fleas *Xenopsylla brasiliensis* and *X. cheopis* appear to be mainly responsible for the persistence of the reservoir in the East African highlands ; *R. rattus* and *X. cheopis* play this role in Madagascar. The gerbils (*Tatera* and *Desmodillus*) and their burrow fleas *X. philoxera* and *X. piriei* are the main reservoirs of plague in southern Africa. Within these areas, *Pasteurella pestis* finds an environment suitable for its continued survival ; the conditions seem to be comparable to those defined as obtaining in endemic centres in India. Elsewhere in Africa such endemic centres do not appear to exist.

Introduction

The Joint OIHP/WHO Study-Group on Plague, at its second session, held in Paris in October 1948, recommended that a WHO team should investigate the incidence of wild-rodent plague in Africa.[a] The proposal was formulated in more detail by Dr. P. C. C. Garnham[b] for consideration at the first session of the WHO Expert Committee on Plague, which was held in Geneva in September 1949. The committee decided[c] to obtain information on the plague position in Africa, with special reference to wild-rodent plague, by distributing a questionnaire to all African territories, in order to assist the committee in deciding whether a survey by a WHO team should be undertaken. A questionnaire (see Annex 1, page 697) was drafted at the meeting and circulated in 1950. The replies provide information of great value and give a clear picture of the plague position over the period 1935-49.

The history of plague in Africa up to 1934 is covered by the detailed report by Jorge,[21] which was based upon an inquiry conducted by the Permanent Committee of the Office International d'Hygiène Publique (OIHP) as a result of discussions at the International Conference of Representatives of the Health Services of Certain African Territories and British India, held in Cape Town, November 1932. This inquiry did not include Madagascar as the epidemiology of plague in that territory had features of its own which needed special study (Jorge [21]). The gap was, however, filled by a publication by Robic.[38] In the present inquiry, Madagascar is included.

The history of plague in Africa has been reported upon recently by Kaul [23] and Pollitzer.[31] These reports should be consulted as the ground covered by them is not fully covered in this report.

A critical analysis of all the data has not been attempted. The topics singled out for particular attention are : (1) the geographical distribution of human plague (location of outbreaks over the period 1899-1939 compared with the period 1940-9); (2) the incidence of human plague in relation to climate (temperature and rainfall); (3) the relative importance of the different plague regions in Africa as permanent enzootic centres; (4) the relative importance of wild and domestic rodents in the persistence of enzootic plague.

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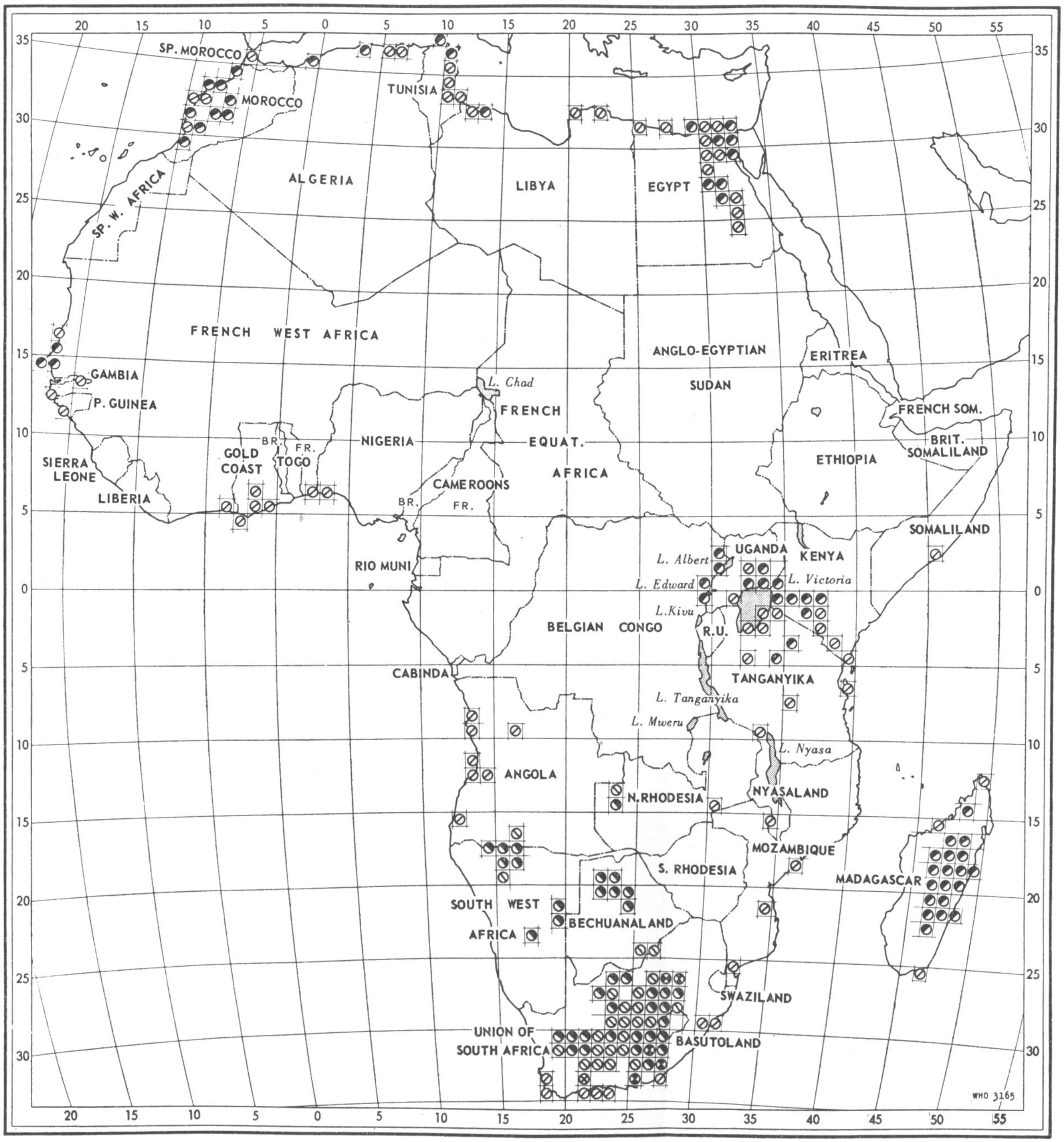
a *Off. Rec. Wld Hlth Org.* **19**, 18

b Unpublished working document WHO/Plague/6

c *Wld Hlth Org. techn. Rep. Ser.* 1950, **11**, 6

FIG. 1. PLAGUE IN AFRICA, 1899-1949



For meaning of symbols, see text (page 667)

Geographical Distribution

Method of plotting. The outline map of Africa (see fig. 1)[d] used for plotting the distribution records (original on the scale of 1:10,000,000) has a superimposed one degree (of latitude and longitude) grid. Given the latitude-longitude co-ordinates of any locality, the occurrence of an event in that locality can be recorded by a symbol in the appropriate " degree square " or " locus ". The symbols in fig. 1 represent the occurrence of one or more plague outbreaks in a locality or localities in the same locus. Each locus can be referred to by a latitude-longitude code. For example, the code for Dakar, latitude 14°40'N, longitude 17°26'W., is N14W17 and the symbol fills the locus square bounded by latitude 14°00'-59'N. and longitude 17°00'-59'W.

The information on outbreak localities has been obtained from a great variety of sources, the chief of which are Johnstone,[20] Low,[26] the *Epidemiological Reports* of the League of Nations,[24, 25] Jorge,[21] Stowman,[43] and Kaul.[23] These sources have, in certain cases, been supplemented by reference to annual reports and by some correspondence. It is not claimed that the records are complete, and inaccuracies will no doubt be found.

The circles represent the occurrence of human plague outbreaks over the period 1899-1949. The black semicircles represent outbreaks between 1940 and 1949. A diagonal line running upwards from left to right indicates that domestic rodents are regarded as playing the major role in maintaining the plague reservoir (murine foci); the diagonal line running from right to left indicates that wild rodents are regarded as being the main plague reservoir (sylvatic foci). In some loci—occurring only in the Union of South Africa—both murine and sylvatic foci are indicated (by crossed lines). In these, the murine foci antedate the sylvatic foci (see Davis [8]).

It will be seen that only one true sylvatic plague area is recognized—that in southern Africa. Jorge [21] made a similar division, but recognized that future investigation might lead to the discovery of true sylvatic foci elsewhere in Africa. He mentioned the occurrence of plague infection in wild rodents in Senegal and East Africa and considered that conditions for sylvatic plague were suitable in North Africa. Since 1935, no evidence has come to hand to indicate that wild desert rodents in North Africa harbour plague.

Present knowledge of the part played by wild rodents in the highlands of East Africa, however, has been clarified by the studies of Devignat [14, 15] in the Lake Albert focus of the Belgian Congo. The classification scheme elaborated by him from this work provides a model for assessing the plague

[d] This map was originally drawn in the Trigonometrical Survey Office, Pretoria, and printed by the Government Printer, Pretoria, in 1950 (Reference No. T.S.O. Misc./798) for use by the Plague Research Laboratory, Union Department of Health, Johannesburg, Union of South Africa.

potential of a plague focus. It is based upon the relative proportions of rodent and flea species and their susceptibility and vector capacity in relation to the routes taken by *Pasteurella pestis* within and between the three main epidemiological planes of activity—sylvatic, domestic, and human—under different circumstances.

Before proceeding to a consideration of the endemicity of plague in Africa an examination will be made of the annual and seasonal incidence of human plague during the period 1935-49, in relation to climate. Such an examination provides certain pointers which will assist in assessing the relative importance of the different plague regions as permanent plague centres in Sharif's sense (Sharif [42]).

Plague and Climate

Annual incidence, 1935-49

Jorge [21] gives the annual incidence of cases of plague in African territories (excluding Madagascar) for the period 1928-34 and the first quarter of 1935. During this period Uganda contributed (in round figures) 15,000, Senegal 10,000, Kenya 3,000, and Egypt 2,000 out of a total of some 35,000 reported cases. The annual incidence fell from about 7,000 during 1928-31 to under 2,000 during 1932-4. Reference to table I, which gives the annual incidence of cases of plague in Africa (including Madagascar), shows that during the 15-year period under review, the general trend has been downwards, particularly from 1946 onwards. In 1949, under 400 cases were recorded for the whole of Africa and Madagascar. This state of affairs can be attributed only in part to measures of control. In Uganda the recession cannot be said to have been influenced by control measures. In Senegal it seems probable that the extensive DDT-campaigns initiated to cope with the epidemic in 1944 (Senegal (Q 1950)) [e] played a significant part in the disappearance of plague from Dakar and its environs, although the low incidence recorded during the preceding years (1936-42) could be interpreted as indicating that natural causes were responsible. There has been a dramatic decline in Madagascar, which followed the introduction of annual mass-vaccination in 1936 (see graph in Kaul [23]). It is hardly necessary to remark that the introduction of residual insecticides and new rodenticides and antibiotics provide such effective means of combating plague that they cannot fail to bring about a marked improvement in the efficiency of control. At the end of 1949 these new methods were coming into more general use.

By the end of 1949, plague had apparently disappeared from North and West Africa and from Uganda. It persisted in the Belgian Congo,

[e] The name of a territory followed by (Q 1950) refers to matter contained in the replies to the WHO questionnaire.

TABLE I. ANNUAL INCIDENCE OF CASES OF PLAGUE IN AFRICA, 1935-49

	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	Total
Madagascar	3,493	2,006	916	630	681	754	272	181	234	184	185	278	274	240	143	10,471
Morocco	41	—	—	6	—	1,099	2,337	583	393	200	811	—	—	—	—	5,470
Uganda	1,995	991	516	383	317	278	218	354	19	7	4	3	1	—	—	5,086
Kenya	139	239	158	28	4	11	781	754	16	13	56	32	55	29	5	2,320
Egypt	40	77	73	11	169	491	14	15	163	644	228	211	15	—	—	2,151
Senegal	419	37	11	2	—	7	—	6	298	640	58	—	—	—	—	1,478
Union of South Africa	355	219	9	92	75	57	76	87	91	50	14	6	35	33	72	1,271
South-West Africa	210	56	51	59	43	49	52	34	233	15	—	—	—	—	8	810
Tanganyika	—	16	135	3	—	—	2	—	—	—	—	—	—	311	18	485
Belgian Congo	19	3	6	26	67	30	73	10	36	22	24	27	41	22	18	424
Bechuanaland Protectorate	2	—	—	—	—	—	—	—	—	302	25	68	2	—	5	404
Algeria	11	10	3	—	2	18	—	—	—	95	11	2	—	—	—	152
Basutoland	9	8	—	—	—	—	—	10	27	—	8	—	—	—	58	120
Tunisia	17	7	3	5	—	12	1	—	—	40	3	—	—	—	—	88
Northern Rhodesia (Barotseland)	—	—	9	—	—	4	—	13	5	3	—	—	1	7	2	44
Angola	15	—	2	—	—	—	—	—	—	—	—	—	—	—	—	17
Tripolitania	—	—	—	—	—	12	—	—	—	—	—	—	—	—	—	12
Nyasaland	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	4
Total	6,765	3,669	1,892	1,245	1,362	2,822	3,826	2,047	1,515	2,215	1,427	627	424	642	329	30,807

in Kenya and Tanganyika, in Madagascar, and in the territories in the southern African enzootic area (Northern Rhodesia, South-West Africa, Bechuanaland Protectorate, the Union of South Africa, and Basutoland). As will be shown later, factors favouring the persistence of murine foci seem to be present in certain parts of East Africa and Madagascar, and of sylvatic foci in southern Africa. On the basis of the annual incidence alone, therefore, there are indications that certain areas in Africa are to be regarded as providing the complex of factors which allow plague to persist in India (Sharif [42]).

Plague seasons in Africa

In this article, an attempt has been made to interpret the seasonal incidence and persistence of plague in terms of climatic influences on the same lines as has been done for India (Plague Research Commission; [29, 30] Brooks; [5] White; [47] Sharif [42]). In general, warm moist weather is associated with a higher incidence of rat plague, a higher flea-index, and a higher incidence of human infections. Hot, dry weather results in a reduction in the flea-index, and a decrease in the incidence of rat and human plague. In India, mean monthly temperatures of 80°-85°F (26.7°-29.4°C) combined with a saturation deficiency of 0.30 inch (7.62 mm) or more (Brooks [5]) were accompanied by a sharp fall in human infections. This has become the " textbook " explanation of the seasonal incidence of both murine and human plague and it provides a point of departure for evaluating climatic influences on the incidence of human plague.

Different combinations of temperature and humidity in the flea's immediate environment have a profound effect on the length of life, on the duration of the period of development (see Sharif [41]), on the activity of fleas (Sharif [42]), and in all probability on their vector efficiency (see Burroughs; [6] Devignat [15]). The standard meteorological observations, measuring as they do the macroclimate to which man is exposed in the open air and in the shade, do not necessarily bear any definable relation to the microclimate in habitations, where man usually becomes infected, or to the ecoclimate of rats and their fleas.

Petrie & Todd [28] and Wakil [45] in Egypt and Robic [38] in Madagascar have demonstrated that the conclusions reached in India on the relation of prevailing atmospheric conditions to plague incidence are also of general validity in these two countries. Roberts [36] has studied the relation of rainfall to the seasonal incidence of plague in a rural area on the southern slopes of Mount Kenya. Good rains ensured good crops, which provided abundant food, which in turn stimulated rat breeding and an increase in plague incidence. The question does not seem to have been studied elsewhere in Africa.

Material used in the survey

The mean monthly plague incidence (the percentage of total cases, 1935-49) in the various territories is compared with " normal " monthly means of temperature and rainfall. For the most part the meteorological data have been taken from published reports of " normals ". The meteorological stations have been selected as far as possible from within a recognized plague area. The assumption, however, that those selected provide the best measure of conditions in the plague area must be guarded against.

KEY TO FIG. 2-15

Fig. 2. Monthly plague incidence (1899-1915) compared with climatic normals for Alexandria, Egypt.

Fig. 3. Monthly plague incidence (1899-1915) compared with climatic normals for Asyût, Egypt.

Fig. 4. Monthly plague incidence in Algeria (1935-49) compared with climatic normals for Algiers Port.

Fig. 5. Monthly plague incidence for Casablanca region (1940-5) compared with climatic normals for Casablanca, Morocco.

Fig. 6. Monthly plague incidence in Marrakesh and Oued Zem (1940-5) compared with climatic normals for Marrakesh, Morocco.

Fig. 7. Monthly plague incidence in Senegal (1935-45) compared with climatic normals for Cap Vert, Dakar.

Fig. 8. Monthly plague incidence in the Belgian Congo (1928-49) compared with temperature at Irumu (1949) and rainfall normals for Nioka, Lake Albert area.

Fig. 9. Monthly plague incidence in Uganda (1935-49) compared with climatic normals for Kampala.

Fig. 10. Monthly plague incidence in Kenya (1935-49) compared with climatic normals for Nakuru.

Fig. 11. Monthly plague incidence in Tanganyika (1935-49) compared with climatic normals for Tabora.

Fig. 12. Monthly plague incidence in Madagascar (1935-49) compared with climatic normals for Tananarive.

Fig. 13. Climatic normals for Tamatave, Madagascar (only sporadic cases of plague).

Fig. 14. Monthly plague incidence in the Union of South Africa (1935-49) compared with climatic normals for Kroonstad.

Fig. 15. Monthly plague incidence in the Bechuanaland Protectorate (1935-49) compared with temperature (1944-5) and rainfall normals for Maun, Ngamiland.

FIG. 2

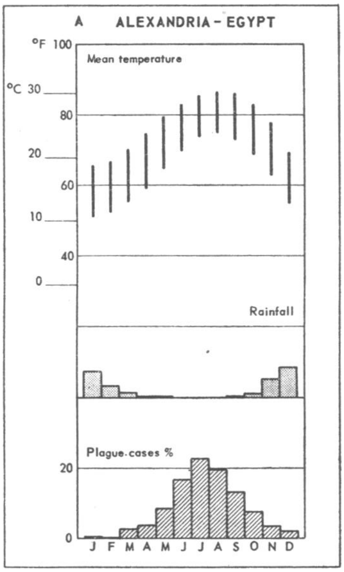


FIG. 3

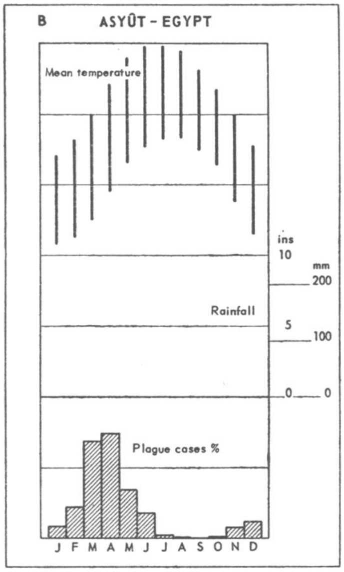


FIG. 4

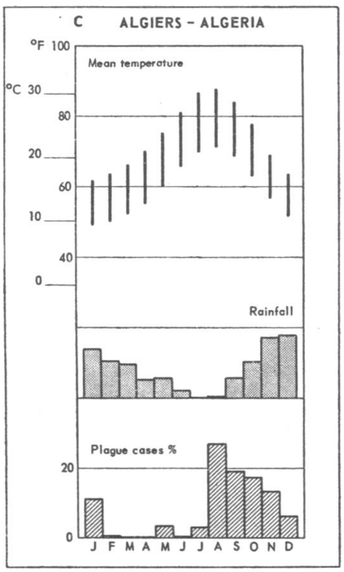


FIG. 5

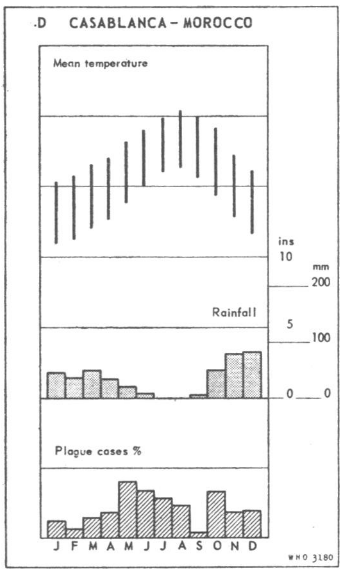


FIG. 6

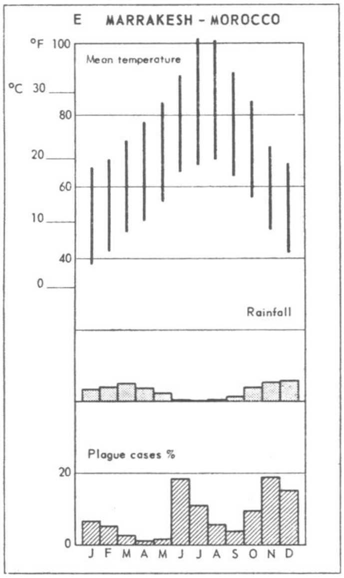


FIG. 7

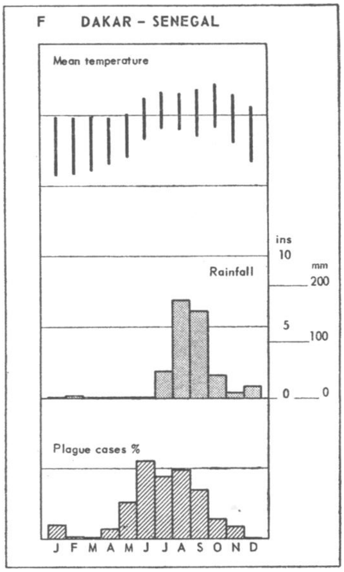


FIG. 8

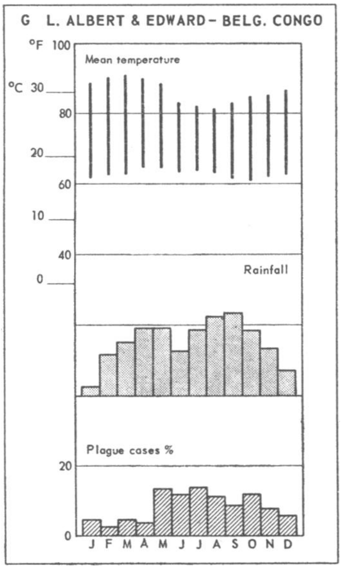


FIG 9

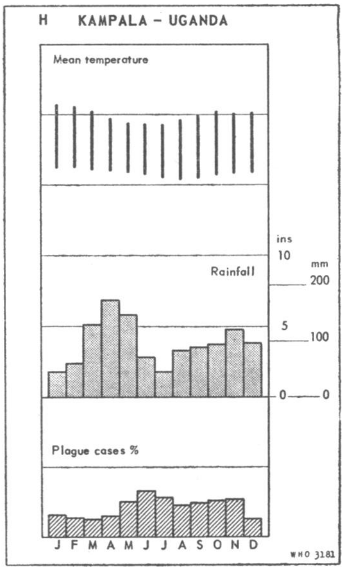


FIG. 10

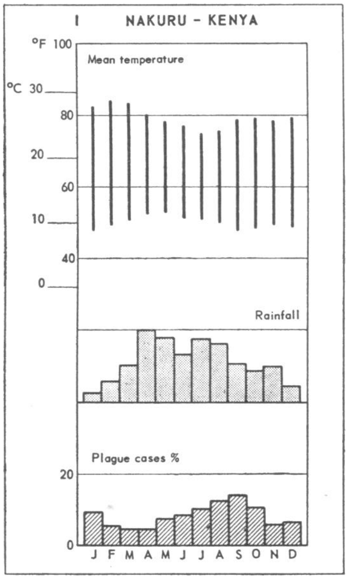


FIG. 11

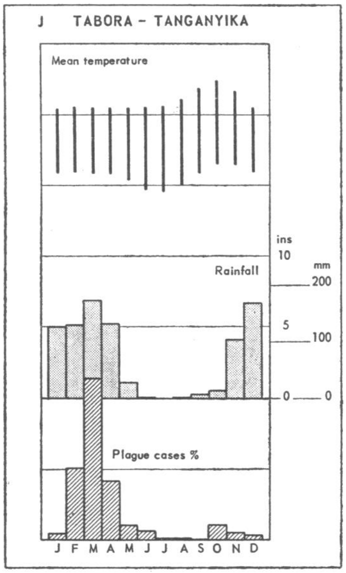


FIG. 12

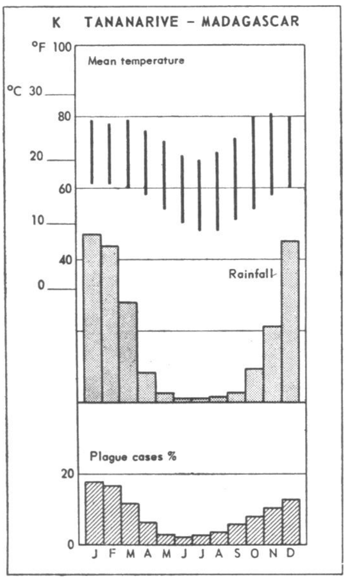


FIG. 13

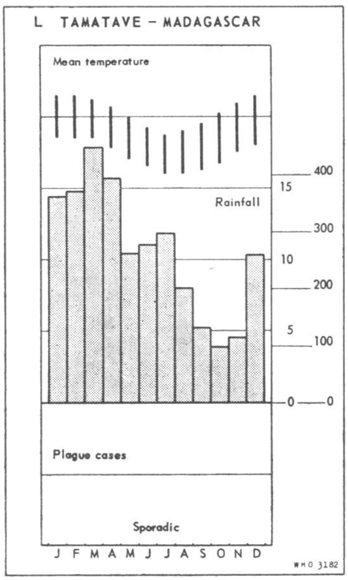


FIG. 14

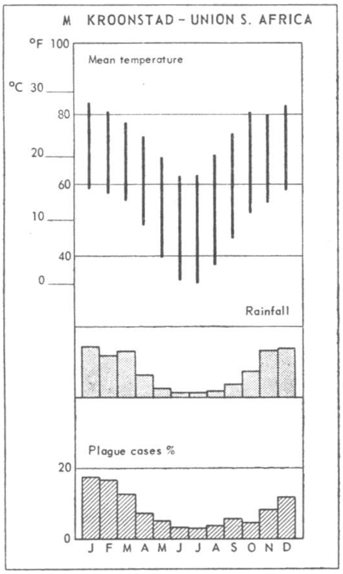
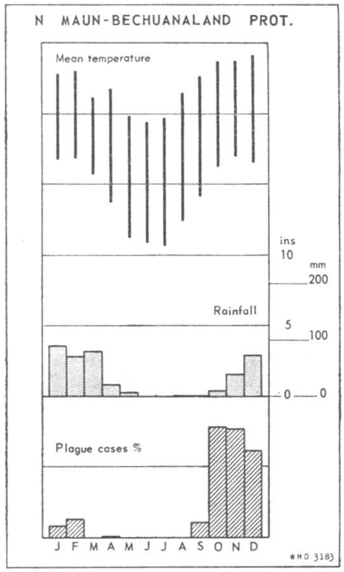


FIG. 15



In the series of diagrams (fig. 2-15), mean monthly maximum and minimum temperatures are represented by the thin vertical lines in the upper part of the diagrams. The mean monthly temperature is equidistant between the extremes. The broader lines below the temperature represent mean monthly rainfall. The mean monthly plague incidence appears below the climatic chart; the data used are given in tables II-XIII.

North Africa

Egypt (see table II and fig. 2-3). The climatic régime of the coastal regions of North Africa is one of wet winters and dry summers (Mediterranean climate). In Egypt, the Mediterranean climate prevails only on the coast, at Alexandria and Port Said. Even here the rainfall is very low. To the south, one passes into the desert climate characteristic of Cairo and Middle and Upper Egypt where there is practically no rain. The absence of rain in Middle and Upper Egypt would probably preclude enzootic plague were it not for the Nile irrigation system which provides soil moisture, which must have an important influence on the life cycle of rat fleas.

During the years 1935-49 epidemics occurred in Asyut (Upper Egypt), Cairo, Port Said, and Alexandria. Petrie & Todd [28] and Wakil [45] have analysed the climatic relations to the plague season in different parts of

TABLE II. FOUR-WEEKLY INCIDENCE OF PLAGUE IN EGYPT, 1935-49

Year	Four-week period													Total
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	
1935	1	2	—	5	16	5	5	—	1	—	1	1	3	40
1936	11	9	11	28	4	3	—	—	3	2	3	2	1	77
1937	1	1	4	48	14	1	1	—	—	—	2	—	1	73
1938	2	—	—	1	5	3	—	—	—	—	—	—	—	11
1939	1	50	29	57	30	2	—	—	—	—	—	—	—	169
1940	20	89	158	153	66	4	1	—	—	—	—	—	—	491
1941	2	2	—	—	—	—	7	2	1	—	—	—	—	14
1942	—	—	—	—	—	1	3	2	1	—	—	7	1	15
1943	—	—	—	—	—	—	1	2	1	—	1	30	128	163
1944	78	29	40	118	222	96	36	11	6	—	6	2	—	644
1945	—	2	—	39	58	59	41	17	4	1	3	1	3	228
1946	1	7	7	36	42	44	32	28	11	2	1	—	—	211
1947	—	—	—	—	2	2	7	4	—	—	—	—	—	15
1948	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1949	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	117	191	249	485	459	220	134	66	28	5	17	43	137	2,151
Mean four-weekly incidence %	5.4	8.9	11.6	22.5	21.3	10.2	6.2	3.1	1.3	0.2	0.8	2.0	6.4	

Egypt. The plague season is shorter and starts earlier (peak in March-April) in Upper Egypt and is later and more protracted on the coast (peak in July and season extending from about May to September). Intervening areas are intermediate between the two extremes. Temperature is regarded as the main controlling factor; for Egypt as a whole, the months of plague prevalence have a temperature range of 64.5°-82.5°F (18°-28°C) and the months of maximum plague prevalence a range of 73.5°-77.0°F (23°-25°C) (Wakil [45]).

In fig. 2 and 3, for Alexandria and Asyut respectively, the plague figures are those for the period 1899-1915 as given in Wakil.[45] During 1939-40, the majority of cases were contracted in the region of Asyut; in 1944-5, in Suez and Port Said; and in 1946, in Alexandria. Comparison of the four-weekly incidence figures (see table II) with fig. 2 and 3 for Alexandria and Asyut show that the seasonal incidence during the period 1935-49 accords with previous years.

Comparison of the chart for Asyut with that for Marrakesh, Morocco, (fig. 6) shows that the temperature régimes for the two areas are very similar. Yet the monthly plague incidence is dissimilar. Thus, at the outset of this analysis, the investigator is brought up against the existence of unknown factors—some of which may indeed be climatic—which make a " rule of thumb " criterion impossible to apply in all circumstances.

Tunisia and Algeria (see fig. 4). These two territories have typical Mediterranean climates with rather cold, wet winters and hot, dry summers, but Tunisia has the lower rainfall. Plague was not very prevalent (Pollitzer [31]).

The climatic régime of Algeria may be compared with that of Alexandria: Algeria has a heavier rainfall and is colder in winter and not quite so hot in summer. The plague season, however, is more clear-cut than in Alexandria. Incidence is highest in August, which is the hottest month; plague then declines with the increased rainfall and falling temperatures from September onwards. Algeria (Q 1950) notes that the flea-index is inversely proportional to rainfall (i.e., fewer fleas in the winter). This would mean that fleas would be most numerous in the hot, rainless months of July and August. The higher flea-index is thus closely related to the start of the plague season. It may be noted that the mean monthly temperature is under 80°F (26.7°C) in August, the critical limit according to Brooks.[5]

Morocco (see table III and fig. 5-6). Between 1940 and 1945, epidemics took place in three main regions : Casablanca, Marrakesh, and Agadir. The month of highest incidence in Morocco as a whole is in June (16.5% of all cases); September has the lowest incidence (2.3%). Casablanca and Marrakesh are climatically very different, the former being more equable and the latter having great extremes of heat and cold. The plague incidence and climatic conditions of the two regions have for purposes of comparison been tabulated and figured separately (fig. 5 and 6). It will be noted that plague is most prevalent at Casablanca in May and at Marrakesh in June and that in both areas there are two peaks during the year—namely, in May-June and October at Casablanca and in June-July and November at Marrakesh. The hot weather of midsummer seems to have a depressing effect on plague incidence in both areas.

A factor influencing the epidemiology of plague in Morocco is the important part played by human parasites (*Pulex irritans* and *Pediculus humanus corporis*) in the inter-human transmission of plague (Delanoë;[13] Blanc & Baltazard[4]). Murine epizootics initiate sporadic human infections and these are followed by inter-human transmission which may continue after the rat epizootic has died down.

TABLE III. MONTHLY INCIDENCE OF PLAGUE IN MOROCCO, 1940-45 *

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1940	—	—	—	91	36	58	15	10	26	166	370	327	1,099
1941	237	210	202	252	301	370	322	234	59	53	66	31	2,337
1942	25	17	94	34	85	123	13	32	18	54	38	50	583
1943	13	19	24	77	74	27	7	6	3	95	45	3	393
1944	14	5	1	2	32	45	7	5	6	27	10	46	200
1945	35	12	60	14	110	270	174	112	13	11	—	—	811
Total	324	263	381	470	638	893	538	399	125	406	529	457	5,423
Mean monthly incidence (%)	6.0	4.8	7.0	8.7	11.8	16.5	9.9	7.4	2.3	7.5	9.8	8.4	

* One outbreak of plague occurred in the spring of 1935 at Ahmar (Safi, Marrakesh) ; no case of plague was reported in the years 1936-9 and 1946-9.

It is of interest to note that the percentage of rats infested by *Xenopsylla cheopis* at Casablanca (1933 and 1934) was highest in June-July and in October (Ristorcelli[33]), the annual curve corresponding fairly closely to the seasonal incidence of plague. This suggests that infestation of man with human parasites follows the same rhythm as infestation of rats with *X. cheopis.*

West Africa

Senegal (see table IV and fig. 7). The most prominent feature of the seasonal epidemiology of plague in Senegal is the sharp rise after the dry period January-February (when the dry harmattan winds blow) to a peak in June before the onset of the rainy season during July-September. There is a noticeable recession in the two hottest months of the year—namely, September and October. The rise in temperature and relative humidity before

TABLE IV. MONTHLY INCIDENCE OF PLAGUE IN SENEGAL, 1935-45

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1935	6	2	2	30	70	104	89	90	23	1	1	1	419
1936	1	1	—	2	6	8	11	6	—	2	—	—	37
1937	—	—	—	1	3	5	2	—	—	—	—	—	11
1938	—	—	—	—	—	2*	—	—	—	—	—	—	2
1939	—	—	—	—	—	—	—	—	—	—	—	—	—
1940	—	—	1	—	1	5	—	—	—	—	—	—	7
1941	—	—	—	—	—	—	—	—	—	—	—	—	—
1942	—	—	—	—	—	—	—	5	1	—	—	—	6
1943	—	—	—	—	72	167	41	10	1	—	7	—	298
1944	—	—	—	5	2	37	117	175	177	79	45	3	640
1945	54	3	1	—	—	—	—	—	—	—	—	—	58
Total	61	6	4	38	154	328	260	286	202	82	53	4	1,478
Mean monthly incidence (%)	4.1	0.4	0.3	2.6	10.4	22.2	17.6	19.4	13.7	5.5	3.6	0.3	

* Total for the year given as 2 ; placed in June for convenience.

the rains seems to favour human-plague transmission, which is checked by high temperatures at the end of the rainy season (October).

During 1944, 7,477 rodents were examined for plague : 8 out of 543 in May, 49 out of 1,448 in June, 5 out of 1,300 in July, and 2 out of 208 in September proved positive (Senegal (Q 1950)). The murine epizootic for that year reached its peak in June, whereas human plague was at its height in July-September (table IV). It has been suggested that inter-human transmission by the common hut-floor flea *Synosternus pallidus* (which is scarce on rats) may occur (Roubaud;[39] Kartman[22]) although experimentally this species was not very efficient as a vector from rodent to rodent (Advier[1]). No case of human or murine plague has come to light since 1945, and it is possible that the introduction of DDT into the control programme in 1944 and its regular use since will stamp out the disease.

TABLE V. MONTHLY INCIDENCE OF PLAGUE IN THE BELGIAN CONGO, 1928-49

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1928	—	—	—	—	—	—	—	—	—	—	1	5	6
1929	8	5	—	—	2	10	21	4	2	—	2	—	54
1930	—	—	—	—	1	4	2	7	—	—	2	—	16
1931	—	—	2	—	—	1	—	—	—	—	—	—	3
1932	1	—	—	—	2	1	—	—	—	—	—	1	5
1933	—	—	—	1	—	—	—	—	—	—	—	—	1
1934	—	—	—	1	—	3	3	1	—	—	12	—	20
1935	8	—	1	—	—	1	4	2	2	1	—	—	19
1936	—	—	—	—	1	—	—	—	—	2	—	—	3
1937	—	—	—	—	—	—	—	—	—	4	—	2	6
1938	—	—	10	1	6	5	2	1	—	1	—	—	26
1939	—	1	2	7	14	1	2	6	12	14	5	3	67
1940	—	2	1	1	4	6	7	2	1	4	—	2	30
1941	1	2	—	—	12	13	17	9	5	8	1	5	73
1942	1	1	1	—	3	—	2	—	—	1	—	1	10
1943	—	—	—	—	—	3	1	—	—	19	9	4	36
1944	—	—	1	1	—	2	—	2	13	1	1	1	22
1945	1	1	—	—	1	2	4	5	—	7	2	1	24
1946	1	—	—	1	—	3	4	13	2	—	3	—	27
1947	—	1	6	1	21	—	—	3	7	—	1	1	41
1948	1	—	1	4	4	4	1	1	1	1	2	2	22
1949	2	—	1	2	1	3	3	3	—	—	1	2	18
Total	24	13	26	20	72	62	73	59	45	63	42	30	529
Mean monthly incidence (%)	4.5	2.5	4.9	3.8	13.6	11.7	13.8	11.2	8.5	11.9	7.9	5.7	

The sharp seasonal demarcation in the incidence of human plague may mean that murine plague has a rather tenuous hold during the off-season. This would mean that control measures applied vigorously during this season might break the transmission cycle.

Gold Coast and Nigeria. No murine or human plague has been reported from the Gold Coast since 1924, nor from Nigeria since 1931. Local ecological factors are evidently insufficient to foster the permanent survival of *Pasteurella pestis* among the rats and their fleas in the uniformly hot, moist climate of the west coast. (See Tamatave (Robic [38]).)

Angola. No murine or human plague was recorded during the period 1935-49 in the ports or inland centres where sporadic outbreaks, originating from the ports, had previously occurred. In the Bas Cunene sylvatic-plague area, 15 cases were reported in 1935 (Ribeiro [32]) and 2 in 1937 (Angola [2]). Plague was prevalent at these times across the border in Ovamboland.

East Africa

Plague was known in the East African highlands before the present pandemic (Thornton;[44] Roberts;[34] Hopkins;[18] Baker [3]). Parts of the region evidently provide conditions which favour the persistence of enzootic plague. The seasonal distribution of human plague is much more uniform than in the areas so far considered. The equatorial climate at relatively high elevations 4,000-6,000 feet (1,200-1,800 metres) has two rainy seasons and rather slight variations in mean temperatures throughout the year, with a daily range from cool nights to fairly hot days. Such conditions approximate rather closely to those regarded by Sharif [42] as being associated with endemic centres of plague in India.

Belgian Congo (see table V and fig. 8). In the Belgian Congo, plague is known only from the mountainous country flanking Lake Albert and Lake Edward on the west. Sporadic cases occur in the scattered villages of the forest and bush country. Plague has never reached epidemic proportions. The case incidence is lower between December and April and higher between May and November. There is a slight recession in August and September. Periods of lower incidence correspond to the drier times of the year and the first months of the long rainy season which follows the dry season of December and January. Throughout the year the climate varies little, although the daily range of temperature is fairly wide, giving hot days and cool nights. The climatic régime is essentially similar to that in other parts of the equatorial highlands in Uganda and Kenya. Although the Congo figures for seasonal incidence are based upon a total of only 529 cases, their seasonal distribution is very close to that of Uganda, in which the figures are based upon 5,086 cases.

TABLE VI. MONTHLY INCIDENCE OF PLAGUE IN UGANDA, 1935-49

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1935	68	49	30	105	189	338	255	205	199	224	252	81	1,995
1936	50	41	62	72	147	130	105	83	91	73	87	50	991
1937	38	32	44	22	47	44	44	35	58	47	68	37	516
1938	31	25	16	7	17	26	54	55	48	68	28	8	383
1939	19	28	25	14	19	50	50	25	31	22	17	17	317
1940	21	21	12	22	25	16	21	22	14	39	44	21	278
1941	23	6	12	10	7	9	11	14	35	28	27	36	218
1942	59	57	37	40	50	39	35	9	5	15	4	4	354
1943	—	—	6	—	2	5	—	4	—	—	—	2	19
1944	—	—	4	—	—	1	—	—	—	1	1	—	7
1945	1	—	—	1	2	—	—	—	—	—	—	—	4
1946	—	—	—	—	2	1	—	—	—	—	—	—	3
1947	—	—	1	—	—	—	—	—	—	—	—	—	1
1948	—	—	—	—	—	—	—	—	—	—	—	—	—
1949	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	310	259	249	293	507	659	575	452	481	517	528	256	5,086
Mean monthly incidence (%)	6.1	5.1	4.9	5.8	10.0	13.0	11.3	8.9	9.5	10.2	10.4	5.0	

Uganda (see table VI and fig. 9). As already noted, the seasonal incidence of plague in Uganda is similar to that in the adjoining region in the Belgian Congo. The plague endemic area is, however, very much more extensive. Hopkins [18] notes that all the endemic areas in Uganda are located in the over 45 inches (1,150 mm) rainfall area, though they do not exist throughout it.

Kenya (see table VII and fig. 10). Climatic conditions in Kenya resemble those in Uganda and in the Lake Albert and Lake Edward highlands, but

TABLE VII. FOUR-WEEKLY INCIDENCE OF PLAGUE IN KENYA, 1935-49

Year	Four-week period													Total
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	
1935	—	—	2	—	11	1	—	29	25	29	10	7	25	139
1936	14	11	12	23	41	34	—	22	13	28	11	18	12	239
1937	20	8	3	5	7	43	—	23	13	21	5	10	—	158
1938	—	4	3	2	1	—	—	10	4	2	1	1	—	28
1939	1	3	—	—	—	—	—	—	—	—	—	—	—	4
1940	—	6	—	—	1	—	—	—	1	1	—	— 2 —		11
1941	—	9	1	—	6	42	53	73	119	183	137	65	93	781
1942	146	80	71	33	65	68	84	80	50	43	24	6	4	754
1943	6	1	—	2	—	—	—	3	2	1	—	—	1	16
1944	—	1	—	—	—	—	2	1	—	6	—	2	1	13
1945	2	1	—	—	1	1	12	12	15	7	5	—	—	56
1946	6	1	—	6	—	1	2	—	3	7	6	—	—	32
1947	—	6	2	13	2	6	8	6	3	—	2	6	1	55
1948	4	3	5	1	—	—	1	7	3	1	2	—	2	29
1949	1	—	—	—	1	2	1	—	—	—	—	—	—	5
Total	200	134	99	85	136	198	163	266	251	329	203	116	140	2,320
Mean four-weekly incidence (%)	8.6	5.8	4.3	3.7	5.9	8.5	7.0	11.5	10.8	14.2	8.75	5.0	6.0	

owing to topographical differences due to the Rift Valley and the high mountains they are more varied, semi-arid areas being interspersed with more humid ones. Roberts [36] studied a small epidemic of plague on the slopes of Mount Kenya at Keruguya. He gives a map showing that the highest plague incidence was in the over 45 inches (1,150 mm) rainfall area on the south-western slopes of Mount Kenya; plague incidence rose at the time of the harvest and was highest between the long and the short rainy seasons, but cases were recorded in all months.

Tanganyika (see table VIII and fig. 11). In contrast to the fairly uniform distribution of human-plague incidence in the previously mentioned territories in the equatorial highlands, the tropical savanna climate of Tanganyika is inimical to human plague for about eight months of the year.

TABLE VIII. MONTHLY INCIDENCE OF PLAGUE IN TANGANYIKA

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1935	—	—	—	—	—	—	—	—	—	—	—	—	—
1936	9	3	1	3	—	—	—	—	—	—	—	—	16
1937	—	67	33	19	11	4	—	1	—	—	—	—	135
1938	—	—	—	—	—	3	—	—	—	—	—	—	3
1941	—	—	—	—	—	—	—	2	—	—	—	—	2
1948	—	23	173	59	9	4	3	—	1	22	10	7	311
1949	—	5	13	—	—	—	—	—	—	—	—	—	18
Total	9	98	220	81	20	11	3	3	1	22	10	7	485
Mean monthly incidence (%)	1.9	20.2	45.4	16.7	4.1	2.3	0.6	0.6	0.2	4.5	2.1	1.4	

Reference to fig. 11 shows that there is a well-marked plague season extending from February to April, which corresponds to the single rainy season. The hot weather from August to November is untempered by rains and is thus very dry. There seems to be no doubt that this hot, dry period is responsible for a dramatic lowering of the incidence of human-plague transmissions. The epidemiology of plague in Tanganyika is characterized by long intervals when no plague occurs (see Jorge [21] and table I). The figures used here refer mainly to the Singida area (Central Province) and to the epidemics of 1937 and 1948-9. The situation in Tanganyika, on account of the sharp annual and seasonal variations, is not suggestive of long-standing, persistent, murine foci, and it is possible that endemic centres in Kenya and Uganda have contributed in the past to the starting of epidemics. On the other hand, the situation could be explained by assuming that a sylvatic reservoir exists, whose host population is subject to periodic fluctuations in numbers, as in southern Africa.

Madagascar (see table IX and fig. 12-13). Robic [38] has pointed out that the hot, damp climate prevailing at Tamatave (and other ports on the east coast) is unfavourable for the persistence of plague, whereas the relatively cool, moist conditions of the central plateau are ideal. The climatic diagrams for Tananarive and Tamatave (fig. 12 and 13) bring out the contrast. The mean monthly maximum temperature at Tananarive barely touches 80°F (26.7°C) in mid-summer and the mean monthly minimum just reaches 50°F (10°C) in midwinter. The heavy rainfall at the port of Tamatave is paralleled on the

TABLE IX. MONTHLY INCIDENCE OF PLAGUE IN MADAGASCAR, 1935-49

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1935	510	491	433	209	128	95	112	138	232	293	345	507	3,493
1936	501	382	206	96	48	38	26	83	104	160	186	176	2,006
1937	170	219	114	57	45	23	25	32	48	59	67	57	916
1938	72	85	57	29	16	5	22	33	60	70	73	108	630
1939	79	77	52	33	16	23	21	25	34	69	108	144	681
1940	143	140	130	59	22	12	19	24	41	48	68	48	754
1941	49	60	38	20	7	3	3	8	12	16	29	27	272
1942	22	23	19	16	6	0	0	7	8	14	27	39	181
1943	46	38	40	16	1	4	4	4	5	13	32	31	234
1944	38	31	10	12	2	1	2	14	5	14	20	35	184
1945	27	19	17	43	8	2	1	5	5	11	15	32	185
1946	47	25	35	11	5	2	4	4	19	28	51	47	278
1947	56	59	25	12	5	12	11	4	13	6	18	53	274
1948	61	46	28	21	11	3	1	7	13	13	15	21	240
1949	29	21	11	13	4	2	4	4	17	20	13	5	143
Total	1,850	1,716	1,215	647	324	225	255	392	616	834	1,067	1,330	10,471
Mean monthly incidence (%)	17.7	16.4	11.6	6.2	3.1	2.1	2.4	3.7	5.9	8.0	10.2	12.7	

TABLE X. MONTHLY INCIDENCE OF PLAGUE IN THE UNION OF SOUTH AFRICA, 1935-49

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1935	39	53	64	67	34	19	9	1	10	17	13	29	355
1936	45	50	39	6	15	19	4	8	17	8	5	3	219
1937	—	3	3	1	—	—	—	1	—	1	—	—	9
1938	3	13	6	19	23	4	2	1	2	—	5	14	92
1939	10	17	20	6	—	—	1	9	1	—	10	1	75
1940	1	3	4	12	4	1	1	7	4	3	13	4	57
1941	35	16	3	4	—	—	10	—	1	3	2	2	76
1942	9	8	29	13	1	1	—	—	—	5	3	18	87
1943	27	19	5	—	—	—	—	8	2	2	4	24	91
1944	14	3	1	—	4	—	—	2	17	2	6	1	50
1945	—	3	1	6	1	—	—	—	—	1	2	—	14
1946	—	—	—	1	—	—	—	1	—	—	3	1	6
1947	2	7	2	—	—	3	3	—	—	—	11	7	35
1948	11	3	7	—	—	—	—	—	1	3	1	7	33
1949	9	13	—	—	3	11	10	9	12	2	2	1	72
Total	205	211	184	135	85	58	40	47	67	47	80	112	1,271
Mean monthly incidence (%)	16.1	16.6	14.5	10.6	6.7	4.6	3.1	3.7	5.3	3.7	6.3	8.8	

plateau at Tananarive only in the months of January-April. For the rest of the year, at Tamatave appreciable amounts of rain fall each month (range 2-5 inches (50-125 mm)) but on the plateau there is practically none until December. The monthly incidence of human plague follows the rhythm of annual rainfall and temperature, the rainless, cool winter being the season of lowest incidence. The rise in mean temperature from about 60°F (15°C) after midwinter to about 70°F (21°C) towards midsummer brings with it a rise in plague incidence, and seems to be more closely connected than rainfall (or relative humidity) with human-plague transmissions, probably, as Robic [38] indicates, through the effect of climate on the activity of rat fleas (*X. cheopis*) in biting human beings. The seasonal incidence of plague in Madagascar is almost identical with that in the high-veld of the Union of South Africa—also a summer rainfall area—but the epidemiological picture is basically different.

Southern Africa

Union of South Africa (see table X and fig. 14). The high-veld climatic régime (typified, for the sake of illustration, by that at Kroonstad in the northern Orange Free State, which has been the scene of a high proportion of plague outbreaks (Davis [8])) is one of fairly hot summers, with intermittent rain, and cold, dry winters (with frost) with an annual range of mean temperature of about 20°F (–7°C). Unlike all the territories so far considered, human infections in the Union of South Africa are usually derived at one remove from the permanent reservoir; that is to say that from the permanent sylvatic foci, transient murine foci are set up which are responsible for the vast majority of human infections. In southern Africa, plague is essentially a rural disease. It is a disease, however, not of country villages but of farms and scattered African agricultural settlements. The indigenous rodents which form the natural reservoir are barely touched by the pastoral and semi-intensive agricultural activities of the sparsely distributed rural population. Plague epizootics among them may be in progress at all times of the year. Secondary infections of domestic rodents may take place also at any time, but transmission to man from the domestic rodent is most frequent during the summer.

During the mild winter of 1949, however, a series of outbreaks took place in the north-western Cape Province during a widespread epizootic among gerbils (*Tatera* and *Desmodillus*). The majority of the infections were contracted directly from gerbil fleas by persons sleeping in the open veld. Such occurrences have been rare, and can be attributed to abnormal epizootic and climatic conditions.

Basutoland (see table XI). The first human outbreak of plague in Basutoland occurred at the end of 1935 as a result of the spread and establishment of rodent plague from the Union of South Africa in the territory immediately adjoining the border. The seasonal incidence of the disease has been similar to that in the Union and calls for no further comment.

South-West Africa. Until 1944, Ovamboland was the only part of South-West Africa to suffer from plague, which manifested itself in a mild form. It was prevalent in the years 1935 and 1943, since when there have been only two further cases (in 1949). Figures on monthly incidence in Ovamboland are not available; plague is, however, most prevalent in the summer months. In December 1944, there was a series of 15 cases of pneumonic plague in the Epukiro Reserve; the infection may have been derived from Ngamiland (Bechuanaland), where an epidemic had been raging (Davis [7]). In 1949, there was an outbreak south of Windhoek, which heralded what almost amounted to an epidemic in 1950 (Innes [19]) in the Windhoek-Gobabis area.

TABLE XI. MONTHLY INCIDENCE OF PLAGUE IN BASUTOLAND, 1935-49

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1935	—	—	—	—	—	—	—	—	—	—	—	9	9
1936	5	3	—	—	—	—	—	—	—	—	—	—	8
1937-41	—	—	—	—	—	—	—	—	—	—	—	—	—
1942	—	10	—	—	—	—	—	—	—	—	—	—	10
1943	7	—	8	—	—	12	—	—	—	—	—	—	27
1944	—	—	—	—	—	—	—	—	—	—	—	—	—
1945	—	—	—	—	—	—	—	—	—	—	8	—	8
1946-8	—	—	—	—	—	—	—	—	—	—	—	—	—
1949	8	—	4	28	8	10	—	—	—	—	—	—	58
Total	20	13	12	28	8	22	—	—	—	—	8	9	120
Mean monthly incidence (%)	16.7	10.8	10.0	23.3	6.7	18.3	—	—	—	—	6.7	7.5	

Bechuanaland Protectorate (see table XII and fig. 15). The plague season in Ngamiland (northern Kalahari) extends from September to February. So far there have been no winter outbreaks. There have been only two outbreaks in the southern Protectorate—in April 1935 and July 1949—both of which were related to concurrent prevalence across the border of the Union of South Africa. The onset of the plague season in Ngamiland is related to a rise in temperature in September at the beginning of summer, two months before the rains set in. It may be noted that huts in the plague area in Ngamiland have been dusted regularly with DDT since 1947.

TABLE XII. MONTHLY INCIDENCE OF PLAGUE IN BECHUANALAND PROTECTORATE, 1935-49

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1935	—	—	—	2	—	—	—	—	—	—	—	—	2
1936-43	—	—	—	—	—	—	—	—	—	—	—	—	—
1944	—	—	—	—	—	—	—	—	—	114	124	64	302
1945	7	—	—	—	—	—	—	—	—	—	—	18	25
1946	—	22	—	—	—	—	—	—	17	12	—	17	68
1947	2	—	—	—	—	—	—	—	—	—	—	—	2
1948	—	—	—	—	—	—	—	—	—	—	—	—	—
1949	5	—	—	—	—	—	—	—	—	—	—	—	5
Total	14	22	—	2	—	—	—	—	17	126	124	99	404
Mean monthly incidence (%)	3.5	5.4	—	0.5	—	—	—	—	4.2	31.2	30.7	24.5	

Northern Rhodesia (see table XIII). As in Ngamiland, the plague season in Barotseland farther north is in the summer months, outbreaks having been recorded between October and February (Davis [10]). There have been only 44 cases since the first outbreak was reported in January 1937. The climatic régime is intermediate between that of the Union of South Africa and that of Tanganyika (see fig. 2). There is a greater range in mean monthly temperature than in Tanganyika, and the rainy season starts earlier.

Plague Endemicity

With the exception of the sylvatic-plague area in southern Africa, the climatic régimes found in plague areas in Africa, therefore, have their parallel in India. In spite of the fact that the information available for African territories is not so full as that for India, one can, by following Sharif's general procedure in delimiting endemic centres, come to some

TABLE XIII. MONTHLY INCIDENCE OF PLAGUE IN NORTHERN RHODESIA (BAROTSELAND), 1937-49

	January	February	March	April	May	June	July	August	September	October	November	December	Total
1937	9	—	—	—	—	—	—	—	—	—	—	—	9
1938-9	—	—	—	—	—	—	—	—	—	—	—	—	—
1940	—	4	—	—	—	—	—	—	—	—	—	—	4
1941	—	—	—	—	—	—	—	—	—	—	—	—	—
1942	—	—	—	—	—	—	—	—	—	6	7	—	13
1943	—	—	—	—	—	—	—	—	—	—	—	5	5
1944	3	—	—	—	—	—	—	—	—	—	—	—	3
1945-6	—	—	—	—	—	—	—	—	—	—	—	—	—
1947	—	—	—	—	—	—	—	—	—	—	—	1	1
1948	5	2	—	—	—	—	—	—	—	—	—	—	7
1949	—	2	—	—	—	—	—	—	—	—	—	—	2
Total	17	8	—	—	—	—	—	—	—	6	7	6	44
Mean monthly incidence (%)	38.7	18.2	—	—	—	—	—	—	—	13.6	15.9	13.6	

useful conclusions about the endemicity of plague in Africa. It may be noted that the equatorial highlands of East Africa and the plateau of Madagascar provide the relatively cool, moist, submontane environments which Sharif [42] singles out as being well adapted to the persistence of murine plague foci. The North African plague areas and Senegal are more difficult to judge. There seems to be no doubt that the Mediterranean littoral is subject to periodic re-invasion, particularly during a war, and that the murine foci so established from time to time are relatively short-lived. In Morocco, there may possibly be small centres in the foothills of the Atlas range in which murine plague has a stronger hold than in the plains or on the seaboard. In Senegal, wild rodents have been invoked as possible reservoirs (page 49 of Jorge [21]), but the available evidence does not seem to support this supposition.

It is noteworthy that the port areas of the African continent are now free from plague—the majority for very many years. It is also noteworthy that plague was relatively short-lived in tropical West Africa (Gold Coast and Nigeria).

In Africa (including Madagascar) as a whole, therefore, endemic centres in Sharif's sense are indicated in parts of the equatorial highlands of East Africa, the plateau of Madagascar (based on murine foci), and in the high-veld and Kalahari of southern Africa (based on sylvatic foci).

As regards epidemicity in those areas subject to seasonal extremes of heat and cold, there is little reason to doubt the importance of moderate temperatures as favouring human-plague transmission. It will be seen from an examination of the charts (fig. 2-15) that, in general, mean monthly temperatures ranging from about 60°-80°F (15°-27°C) are associated with a higher number of human cases. In contrast to these favourable warm conditions, hot and cold weather exert a depressing effect on the frequency of human infections. The effect of hot weather is best seen in Egypt, parts of Morocco, and in Tanganyika, and the effect of cold weather in Madagascar, the Union of South Africa, and Algeria.

The influence of rainfall is less well defined. The endemic centres in the highlands of East Africa and Madagascar receive over 45 inches (1,150 mm) per annum, but excessive humidity is not regularly experienced, partly on account of the fairly wide diurnal range in temperature. These areas are in direct contrast to the muggy, coastal climates—characterized by the tropical coastal areas—where plague has never gained a firm foothold.

In order to clarify the relation between atmospheric conditions and rodent and human plague, the ecology of fleas, especially in regard to their vector capacity, needs to be further studied under different combinations of temperature and humidity.

Hosts and Vectors : The Plague Reservoir

It will be convenient in this section to adopt the classification of Devignat (see section entitled "Geographical distribution" on page 667) in discussing the part played by different species of wild and domestic rodents and their fleas in the infection of man. It is not possible, of course, with the data available, to reduce this relationship to tentative mathematical formulae as Devignat [14, 15] has done for the Lake Albert focus on the Belgian Congo.

Devignat recognizes three planes of plague activity—the sylvatic, the domestic, and the human (he excludes pneumonic transmissions) ; and six modes of transmission—intersylvatic, sylvatic-domestic, interdomestic, sylvatic-human, domestic-human, and interhuman. He notes that three of the above modes are theoretically reversible, namely sylvatic-domestic, sylvatic-human, and domestic-human. I shall restrict the designation

" sylvatic plague " to plague in " free-living " rodents living in a wild environment, and the designation " domestic plague " to plague in habitation-frequenting rodents living in a human environment. " Murine " has been employed in this article in the same sense as " domestic ". Devignat's nomenclature will be followed here.

In most African territories plague is active on the domestic plane, with transmission following the interdomestic and domestic-human routes. A provisional classification of the state of affairs as at the end of 1949 is given in table XIV. In the columns headed " Importance in plague cycle ", an assessment is made of the contribution made by host and vector to the circulation of *Pasteurella pestis* on each plane. The relative importance and interrelation of the different planes is a different matter and will be dealt with separately. In the last column of table XIV, however, the modes of transmission to *man* are indicated.

The sylvatic plane

Southern Africa provides the clearest example of the persistence of plague on the sylvatic plane. The evidence so far gathered shows that plague on the domestic plane is incapable of persisting without periodic re-infection from the sylvatic plane. The strongest link between the two planes is the multimammate mouse (*Rattus (Mastomys) natalensis*,[f] hereafter referred to as *Mastomys*) a species which is equally at home on both planes and almost entirely responsible for the sylvatic-domestic mode of transmission from the gerbil reservoir (mainly *Tatera*) to man, often via domestic rats (*R. rattus*).

The persistence of plague amongst gerbils (*Tatera* and *Desmodillus*) seems to be due to the ability of their two common burrow fleas, *X. philoxera*[g] and *X. piriei* to act not only as vectors but as harbourers of *Pasteurella pestis*. The correspondence between the enzootic-plague area and the distribution of these species is so close that their presence has come to be regarded as an indication of a suitable environment for the persistence of enzootic plague (De Meillon;[11] Davis[8, 9]).

In North Africa, plague seems to be moderately persistent on the domestic plane in the coastal areas, but is apparently reinforced from time to time by introductions (mainly by sea). The semi-arid and arid regions of the Sahara (the bled), containing wild burrowing rodents occupying similar ecological niches to their counterparts in southern Africa, are apparently free from plague. Wassilieff[46] demonstrated that the merion (*Meriones shawi*) was endowed with a natural resistance to plague comparable to that of the Namaqua gerbil (*Desmodillus*) in South Africa. He concluded that the merion was unlikely, on that account, to be a reservoir

[f] Synonym : *R. (Mastomys) coucha*

[g] Synonym : *X. eridos* of authors

TABLE XIV. THE MAIN HOSTS AND VECTORS ASSOCIATED WITH THE PLAGUE RESERVOIR IN AFRICA

Territory	Sylvatic plane			Domestic plane			Human plane		Modes of transmission to man
	dominant host	dominant vectors	importance in plague cycle	dominant hosts	dominant vectors	importance in plague cycle	dominant vectors	importance in plague cycle	
Egypt	—	—	—	*R. rattus* *R. norvegicus*	*X. cheopis*	primary	—	—	domestic-human
Algeria	—	—	—	*R. norvegicus* *R. rattus*	*X. cheopis*	primary	—	—	domestic-human
Morocco	—	—	—	*R. rattus* *R. norvegicus*	*X. cheopis*	primary	*P. irritans* *P. humanus*	considerable	domestic-human interhuman
Senegal	*Cricetomys*	?	slight	*R. rattus* *R. norvegicus*	*X. cheopis*	primary	*S. pallidus*	suspected	domestic-human (?) interhuman
Belgian Congo	*Arvicanthis*	*D. lypusus*	? secondary	*Mastomys* *R. rattus*	*X. brasiliensis* *X. cheopis*	primary	(*Ct. felis strongylus*)	? none	domestic-human
Uganda	—	—	—	*R. rattus* *Mastomys*	*X. brasiliensis* *X. cheopis*	primary	(*Ct. felis strongylus*)	none	domestic-human
Kenya	—	—	—	*R. rattus* *Mastomys*	*X. brasiliensis* *X. cheopis*	primary	—	—	domestic-human
Tanganyika	—	—	suspected	*R. rattus*	*X. brasiliensis*	primary	—	—	domestic-human
Nyasaland	? *Tatera*	? *X. syngenis*	? transient secondary	*R. rattus* *Mastomys*	*X. brasiliensis*	non-persistent	—	—	domestic-human
Madagascar	? *Brachytarsomys*	—	?	*R. rattus*	*X. cheopis*	primary	*Pulex irritans*	unknown	domestic-human
Union of South Africa	*Tatera* *Desmodillus*	*X. philoxera* *D. ellobius ellobius* *X. piriei*	primary	*R. rattus* *Mastomys*	*X. brasiliensis*	primary (transient reservoir)	*Pulex irritans*	slight	sylvatic-human domestic-human interhuman (suspected)
Basutoland	*Tatera*	*X. philoxera*	primary	*R. rattus* *Mastomys*	*X. brasiliensis*	primary (transient reservoir)	—	—	domestic-human
Ovamboland, South-West Africa	*Tatera*	*X. philoxera*	primary	*Mastomys*	*X. brasiliensis*	primary (transient reservoir)	—	—	sylvatic-human (?) domestic-human
Ngamiland, Bechuanaland Protectorate	*Tatera*	*X. philoxera*	primary	*Mastomys*	*X. philoxera*	primary	—	—	sylvatic-human (?) domestic-human
Barotseland, Northern Rhodesia	*Tatera*	*X. philoxera*	primary	*Mastomys*	*X. brasiliensis*	primary (transient reservoir)	—	—	sylvatic-human (?) domestic-human

host. He was under the impression that *Desmodillus* escaped natural infection. This, however, is not the case : *Desmodillus* suffers heavily during plague epizootics, but, on account of its natural resistance, the course of the epizootic is somewhat prolonged.

According to Devignat's studies,[14, 15] the persistence of plague in the Belgian Congo seems to be divided about equally between the sylvatic and the domestic plane. In Kenya and Uganda, the participation of wild rodents has been suspected, but conclusive proof that they make any significant contribution to the maintenance of the plague reservoir has been lacking (Roberts; [37] Hopkins [18]).[h] In Tanganyika, wild rodents have been found infected (Lurz [27]).

The small, transient focus of plague set up in southern Nyasaland which gave rise to four human cases in 1939 is thought to have been the result of an introduced infection, possibly from Beira, (Nyasaland (Q 1950)). Mortality among *Tatera* and *Saccostomus* was observed and plague proved in *R. rattus* and *Mastomys*.

The inclusion of the Barotseland focus (Northern Rhodesia) in the southern African plague region is based largely on the presence there of *X. philoxera*, the common *Tatera* flea whose distribution tallies rather closely with the enzootic area of southern Africa (Davis [10]), as well as on the general similarity of conditions to those in Ngamiland (Bechuanaland). It is not yet known to which " variety " of *Pasteurella pestis* the Barotseland strain belongs. Its reaction to glycerol would indicate whether the focus originated from southern or central Africa, as southern African strains do not ferment glycerol whereas Central African ones do. (See Devignat.[16])

In Senegal, a number of small wild mammals have been found plague-infected. Since 1935, two specimens of *Cricetomys gambianus* have been so found (Senegal (Q 1950)). The available evidence is not sufficient to determine whether the sylvatic plane is significantly involved in Senegal.

The domestic plane

Vectors. *X. cheopis* is the predominant vector in North Africa, Senegal, and Madagascar, and *X. brasiliensis* in East and southern Africa. *X. cheopis* is involved in East Africa, in urban areas (Roberts [35]); it is not, however, concerned in plague transmission in southern Africa, because the urban areas (to which it is almost wholly restricted) are plague-free. It should be added that in the East African region, *X. cheopis* is present as a wild- and domestic-rodent flea in the northern section of the Lake Albert focus and in northern Uganda (where there is little or no plague (Hopkins[18])). *X. brasiliensis* has not been recorded from Madagascar (De Meillon [12]).

[h] Recent studies in Kenya indicate that wild rodents (*Arvicanthis* and *Otomys*) were involved in outbreaks in Nakuru along with *Mastomys* and *R. rattus* (Heisch [17]).

No explanation has yet been given of the predilection of *X. brasiliensis* for rural areas and of *X. cheopis* for urban areas in parts of East and southern Africa.

Hopkins [18] asserts that plague in Uganda originates in certain rural endemic centres (unspecified) and spreads to other rural and to urban areas. *X. brasiliensis* is thus primarily involved in the maintenance of the permanent reservoir (now almost or quite quiescent in Uganda).

In North Africa, Senegal, and Madagascar, *X. cheopis* is concerned in both urban and rural areas. The evolutionary centre of *X. cheopis* was probably in northern Africa and of *X. brasiliensis* in Central and southern Africa (see Davis [7] for a discussion of the host-distribution of *X. brasiliensis* in Ngamiland).

The consensus of opinion indicates that the two species have similar vector capacities. Devignat [15] rates *X. brasiliensis* somewhat lower than *X. cheopis.*

Hosts. Rattus norvegicus has never established itself in the hinterland of Africa (or Madagascar). *R. rattus*, on the other hand, has penetrated deeply. Hopkins [18] traced the spread of *R. rattus* in Uganda. It was recorded in the Belgian Congo (Q 1950) for the first time (1948) at Kasenyi on the western shore of Lake Albert (though it had been present in the Lake Edward focus since at least 1936). In Madagascar, the black variety, *R. rattus rattus*, is said to inhabit forest country in the plateau (Madagascar (Q 1950)), while the grey *R. rattus alexandrinus* is the variety found in and around villages. In Egypt, the white-bellied variety, *R. rattus frugivorus* lives in the open, especially in palms (Wakil [45]). Schwarz [40] discusses the origin of African house-rats with special reference to the different races and considers that some races may be more susceptible to plague than others. Ecological differences, as instanced above, may be important from the point of view of the degree of contact made with indigenous rodents.

The indigenous African house-rat, the multimammate mouse, generally retreats in competition with *R. rattus* but still retains its semi-domestic habits; it is of first importance as a host on the domestic plane and as a link with the sylvatic plane, and vice versa. Although it occurs in Morocco, it has not, apparently, been concerned in plague. It is absent in North Africa and Madagascar, but is closely bound up with plague elsewhere.

Little work has been done on the development of resistance to plague in domestic rodents in enzootic-plague areas. Devignat [14, 15] has shown that *Mastomys* and other rodents vary in susceptibility (as tested by the standard method of Sokhey & Maurice) from year to year. Further work in other areas on these lines seems indicated, especially in view of the epidemiological importance attached to the development of resistance in *R. rattus* in different parts of India in regulating the incidence of enzootic plague.

The human plane

Human fleas (*Pulex irritans*) and lice (*Pediculus humanus*) are held to be more important in the epidemiology of human plague in Morocco than rat-fleas (Blanc & Baltazard [4]). *Synosternus pallidus*, the " human "- or hut-flea of Senegal, may also effect interhuman transmissions (Kartman [22]). The human flea of East Africa, *Ctenocephalides felis strongylus*, although found plague-infected, has no vector capacity (in experimental inter-rodent transmissions) (Devignat [14]). In South Africa, plague was isolated from *Pulex irritans* at the scene of an outbreak in circumstances suggestive of its playing some part in the spread from one person to another. A batch of lice, *Pediculus humanus*, from a plague patient have also been found to contain *Pasteurella pestis.*

Pulex irritans is a common parasite in human habitations in Madagascar (De Meillon [12]), but its role, if any, in the interhuman spread of plague has not been studied.

Modes of transmission

The chief modes of transmission to man have been listed in table XIV (last column). The commonest is, of course, the domestic-human by means of rat-fleas; the interhuman and sylvatic-human are rarer and due to unusual circumstances. Infection of man directly from the sylvatic plane has been observed on a number of occasions in southern Africa. The most recent example has been referred to (see page 687). Outbreaks have been traced to the larger of the small mammals of the veld, spring-hares (*Pedetes cafer*) and hares (*Lepus* sp.), that have been captured for food or handled dead or sick in the veld.

In the Belgian Congo, plague in the rodents in, and in the immediate vicinity of, villages in the Lake Albert focus has been studied (Devignat [14, 15]). No case of sylvatic-human infection is recorded. In the " hut " environment, *Mastomys* is infested by *X. brasiliensis* (or *X. cheopis* in the north and east) and by a few wild-rodent fleas. In the bush it carries mainly wild-rodent fleas, chiefly *Dinopsyllus lypusus. Arvicanthis* has semi-domestic tendencies, but outnumbers *Mastomys* in the bush in much the same proportion as it is outnumbered by *Mastomys* in the huts. The host- and vector-species of huts and bush are about of equal value in the interchange of *Pasteurella pestis* between the sylvatic and domestic planes. Whether either or both play the essential part in maintaining the plague reservoir could be determined only by eliminating the one and seeing whether the other is capable of maintaining the reservoir. In the Union of South Africa, domestic rodents harbour *X. brasiliensis* together with a sprinkling of wild-rodent fleas, and the wild rodents have their own fleas together with a sprinkling of domestic-rodent fleas (Union of South Africa (Q 1950)), with *Mastomys* as the intermediary.

In Madagascar, Senegal, and North Africa there seems to be no such interchange of infection between the domestic and sylvatic planes of more than temporary significance. In Madagascar, the interdomestic mode of transmission is strong and points to the domestic plane as providing the permanent reservoir. This may also apply in Senegal and North Africa.

Further Investigations

There is much scope for further work on plague in Africa, especially on the vector-efficiency of different species of fleas and their ability to remain infective in relation to varied microclimatic conditions. In conjunction with such laboratory study, the ecoclimate in which plague fleas normally live needs exact study, with special reference to the persistence of *Pasteurella pestis.*

An analysis of the geographical incidence of human and rodent plague, aimed at pin-pointing endemic centres especially in East Africa and Madagascar (suspected as containing such permanent endemic centres), is required.

The contribution made by wild rodents to the persistence of plague in Uganda, Kenya, and Tanganyika should be critically assessed on lines similar to those developed by Devignat [14, 15] in the Lake Albert focus of the Belgian Congo. A search for wild-rodent plague in North Africa, using modern techniques of plague detection, remains to be made.

Annex 1

SURVEY OF WILD RODENTS IN AFRICAN TERRITORIES

Questionnaire to Governments

1. Date of last case of human plague in territory.
2. Number of human cases per annum since 1935, giving monthly incidence.
3. Date of last finding of rat plague.
4. Number and species of domestic rats positive to plague since 1935, with total number examined, giving monthly incidence. Method of examination employed.
5. Has plague in the wild rodents been observed in the territory ? If so, state :
   (*a*) how diagnosed
   (*b*) date of occurrence
   (*c*) species of rodent
   (*d*) association with human cases
   (*e*) rodent mortality of any kind
6. How does plague spread in the territory ?
7. Flea vector :
   (*a*) identification of rodent fleas
   (*b*) species incriminated as vector
   (*c*) species suspected as vector

8. Actual geographical location of infection. Map showing geographical location to be attached.
9. Meteorological information on plague area since 1935.
10. What methods of plague control are in routine use ?
11. Publications on the subject may be referred to.

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RÉSUMÉ

Le Groupe mixte OIHP/OMS d'étude de la Peste avait recommandé, lors de sa deuxième session, en 1948, qu'une enquête sur la peste en Afrique fût organisée, pour la période postérieure à 1934. (Une enquête, portant sur la situation jusqu'à cette date, avait été effectuée, dans certaines régions africaines, sous les auspices de l'OIHP.) Le Comité d'experts de la Peste, de l'OMS, reprit cette idée, et à sa demande, un questionnaire fut envoyé par l'OMS à tous les territoires africains, en 1950. Cette enquête avait pour objet d'établir le nombre annuel de cas de peste humaine et de peste des rongeurs, le mode de propagation de l'infection, les espèces de puces vectrices, la localisation géographique des poussées épidémiques et de l'endémie, de réunir des données météorologiques et des informations sur la lutte antipesteuse.

La présente étude est fondée en grande partie sur les réponses à ce questionnaire. L'auteur considère en particulier la répartition géographique de la peste humaine (comparant la période de 1899-1939 à celle de 1940-49), la fréquence de la peste humaine en relation avec le climat, l'importance des diverses zones d'endémie pesteuse d'Afrique comme centres d'infection, l'importance relative des rongeurs domestiques et des rongeurs sauvages dans le maintien de l'enzootie.

La fréquence annuelle de la peste en Afrique a diminué, surtout depuis 1946. Alors qu'en 1935, plus de 6.000 cas avaient été déclarés, 400 seulement ont été enregistrés en 1949. Il semble que la peste ait disparu de l'Afrique du Nord depuis 1949. A la fin de cette année-là, la peste sévissait encore au Congo Belge, dans le Kenya et le Tanganyika, à Madagascar et dans certains territoires de l'Afrique australe.

L'auteur montre que les relations entre le climat et la fréquence de la maladie sont les mêmes en Afrique que dans l'Inde : le climat chaud et humide favorise la propagation de l'infection. A Madagascar, ainsi que dans une région du Kenya étudiée à ce point de vue, on a constaté que la pluie, en assurant de bonnes récoltes, procure aux rats une nourriture abondante ; celle-ci stimule leur multiplication ; celle des puces s'ensuit, ayant pour conséquence la dissémination de l'infection parmi la population. Les climats chauds et secs ou les climats froids sont défavorables au développement de l'infection. Les conditions qui règnent dans les hauts plateaux de l'Afrique centrale et de Madagascar semblent propices à la persistance de la peste chez les rongeurs domestiques ; celles du haut-veld et du Kalahari du sud paraissent entretenir l'enzootie chez les rongeurs sauvages.

L'auteur examine les conditions écologiques que rencontre la peste dans de nombreux territoires africains et résume l'histoire des poussées épidémiques qui s'y sont manifestées au cours de la période envisagée.

La peste peut exister comme infection des rongeurs sauvages, des rongeurs domestiques ou de l'homme, la transmission pouvant s'effectuer de chacun de ces « niveaux » à l'autre. De nombreuses espèces de rongeurs et de puces — que l'auteur énumère — sont responsables de la propagation de la peste dans les diverses régions de l'Afrique et aux divers « niveaux » de transmission.

Les sujets ne manquent certes pas pour de futures recherches sur la peste en Afrique. Il s'agirait en particulier *a)* d'étudier le pouvoir vecteur de diverses espèces de puces, leur infectivité et la persistance de *P. pestis* en fonction du microclimat ; *b)* de repérer les centres permanents d'endémie et d'enzootie pesteuses, en particulier en Afrique orientale et à Madagascar ; *c)* d'étudier le rôle des rongeurs sauvages dans le maintien de la peste en Ouganda, au Kenya et au Tanganyika ; *d)* de rechercher s'il existe des foyers de peste des rongeurs sauvages en Afrique du Nord.

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