Bull. Org. mond. Santé
Bull. Wld Hlth Org. } 1955, **12**, 711-725

A REGIONAL RECONNAISSANCE ON YELLOW FEVER IN THE SUDAN

With Special Reference to Primate Hosts *

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Manuscript received in December 1954

SYNOPSIS

Neutralization-tests with yellow fever virus performed on 666 human sera collected in the southern Sudan imply that yellow fever is still endemic south of the 10th parallel, in the south-west border of the Nuba Mountains, and in the plains west of the Nuba Mountains as far north as El Muglad. Similar tests on bloods from 110 primates revealed a high rate of immunity among both baboons (*Papio* sp.) (94%) and grivet monkeys (*Cercopithecus aethiops*) (77%), and a very low rate (1 in 56) among galagos (*Galago senegalensis*). It would therefore appear that, in contrast to the baboon and the grivet monkey, the galago is not significantly involved in the cycle of the virus.

The epidemiological implications of these findings are discussed.

There is an acceptable explanation for the persistence of yellow fever virus in the extensive rain-forests of Africa and South America. Effective vectors (certain species of mosquito) and susceptible vertebrates (monkeys) have been identified. Both occur throughout the year in adequate numbers to explain the maintenance of the virus in cyclic passage, probably in the

* This study was conducted under the auspices of the Ministry of Health of the Sudan, the Department of Virology of the United States Naval Medical Research Unit No. 3, Cairo, Egypt, and the Division of Medicine and Public Health, of the Rockefeller Foundation, New York, N.Y., USA. Latterly, the Department of Virology of the United States Naval Medical Research Unit No. 3 received aid from the Office of Naval Research through a contract administered by the University of Chicago.

form of wandering epizootics, but the extension of yellow fever, and particularly its manner of persistence in zones beyond the confines of the rain forests in Africa, are not clear. The climatic and biological environments in these zones may vary widely from those of the rain-forests. This applies to both mosquito and primate fauna. Thus the explanation which has been offered for the persistence of the virus in rain-forests becomes invalid or inadequate; at least, the same species of mosquito and primate are not equally and consistently involved. The southern Sudan is a case in point. Species of monkey that have been incriminated as hosts of the virus and are so abundant in the rain-forests of equatorial Africa may not exist or are rare over large areas of the southern Sudan.

How, then, is the virus maintained ? This communication does not pretend to answer the question, but it does give some additional information and impressions regarding suspected animal hosts in a part of this rather vast region.

History of Yellow Fever in the Sudan

It is not within the intended scope of this paper to review in detail the previous literature on yellow fever in the Sudan; for review and reference see Kirk,[5] Mahaffy, Smithburn & Hughes,[8] and Bonnel & Deutschman.[1] Suffice it to state that the wide distribution of immunity to yellow fever among the human population in the southern Sudan was noted by Sawyer & Whitman.[9] The term " silent area " was applied to this region as the disease was not clinically manifest. However, in 1940 the presence of yellow fever was dramatically emphasized by the occurrence in the Nuba Mountains of the most severe and extensive epidemic of yellow fever ever recorded in Africa.[4]

Subsequent immunity surveys (reviewed by Kirk [5]) have further confirmed the original one made by Sawyer & Whitman.[9] In mapping the results of these surveys, Kirk has appropriately taken into consideration the age of the donors giving an immune reaction. Immunity in a child not only narrows the time of infection within the life of the child but also usually provides more accurate guidance in locating the place where the infection was contracted, as children are less likely than adults to have visited places far from their homes. On the basis of immunity in children, yellow fever appears to be endemic in all places sampled lying south of about the 10th parallel and west of the West Nile, with an extension northward including the Nuba Mountains and adjacent western plains.

In the Nuba Mountains region, particularly after the epidemic, high immunity rates were found, and there is little doubt that the man-mosquito cycle was largely, if not uniquely, involved in the epidemic. In other parts of the southern Sudan, however, the lower rate of immunity and the

graded increase with age strongly suggest an endemic situation in which infection is gradually taking place. This further suggests that some cycle other than the man-mosquito cycle may be involved. This possibility had been considered, and at various times animal bloods had been collected and tested for neutralizing antibodies for yellow fever virus. The results of these tests have been compiled by Kirk & Haseeb,[6] and those on the primates are listed below:

Species	*Locality*	*Number positive*	*Number negative*
Cercopithecus aethiops (grivet monkey)	Fung	2	17
Erythrocebus patas (red hussar monkey)	Fung	0	2
	Kau	0	1
Colobus polykomos (colobus monkey)	Imatong Mountains	0	2
Galago senegalensis (bush-baby)	Nuba Mountains	0	10
	Total	2	32

Only two of the 32 primates gave a positive reaction, and these two were among the 17 grivet monkeys included in the collection.

Investigation Methods

Field collections and observations

Three field-collection trips were made. The first was in December 1952, and included the Malakal, Juba, and Torit area (see fig. 1 and table I); during this trip only human bloods were collected. The second was made in February 1953, when the Wau-Gogrial area was visited and, in addition to human bloods, a few specimens from baboons were obtained. The last visit was made during February and March 1954; it covered the western and southern edge of the Nuba Mountains, and the plain country to the west and as far south as the Gogrial area.

The first two visits were made for collecting specimens for the study of viral and rickettsial diseases in general rather than of yellow fever. Only the last trip, which covered some 2,000 miles overland, was for the express purpose of investigating yellow fever; during this journey efforts were directed primarily to surveying the primate population (baboons, monkeys, and galagos) and collecting blood specimens from them and from humans (mainly children) in the same area.

All these expeditions were considered to be of a preliminary or reconnoitring nature, but because it is uncertain when further studies will be pursued it is thought justifiable to record the data and impressions derived from these visits.

The following brief description of the terrain, climate, flora, fauna, and human inhabitants applies to the territory covered during the last visit, when special effort was made to observe and obtain information

FIG. 1. AREA OF INVESTIGATION IN THE SUDAN

The numbers arranged from north to south indicate the location of places where blood specimens were collected ; for explanation, see table I opposite.

on the presence and prevalence of primates, and to collect blood specimens from them.

The overland journey by " jeep " and truck began at El Obeid and the principal points visited are shown by the following numbers on the map; (2) El Nahud, (3) Abu Zabad, (4) Kasha, Salara, and Tukma, (5) Kadugli, (6) El Muglad, (7) Um Dorein, (8) Talodi, (10) Mayen Mission and (11) Gogrial area.

Terrain

From El Obeid southward and skirting the Nuba Mountains, the terrain is monotonously flat. The soil is sandy to clay; in the depressions where water accumulates during the rainy season it is dark brown to

TABLE I. RESULTS OF YELLOW FEVER NEUTRALIZATION TESTS ON HUMAN SERA FROM THE SUDAN

Map reference	Age-group (years)									Year	Tests
	under 15			15 and over			all ages				
	total tested	positive		total tested	positive		total tested	positive			
		(number)	(%)		(number)	(%)		(number)	(%)		
(1) Khartoum	24	1*	4	56	3	5	80	4	5	1952	**
(2) El Nahud	10	0	0	17	2	12	27	2	7	1954	†
(3) Abu Zabad	40	0	0	5	0	0	45	0	0	1954	†
(4) Kasha	11	0	0	11	2	18	22	2	9	1954	†
(4) Salara	26	0	0	0	0	0	26	0	0	1954	†
(4) Tukma	15	1	7	0	0	0	15	1	7	1954	†
(5) Kadugli	23	0	0	1	0	0	24	0	0	1954	†
(6) El Muglad	35	2	6	0	0	0	35	2	6	1954	†
(7) Um Dorein	24	1	4	0	0	0	24	1	4	1954	†
(8) Talodi	25	2	8	0	0	0	25	2	8	1954	†
(9) Malakal	18	8	44	23	8	35	41	16	39	1952	**
(10) Mayen Mission	12	6	50	7	1	14	19	7	37	1954	†
(11) Gogrial area	6	0	0	11	6	54	17	6	35	1953	**
(12) Juba	19	3	16	20	5	25	39	8	21	1952	**
(13) Kaguada	18	1	6	21	5	24	39	6	15	1952	**
(14) Yei	16	1	6	22	8	36	38	9	24	1952	**
(15) Torit	21	4	19	7	0	0	28	4	14	1952	**
(15) Keyala	24	2	8	20	4	20	44	6	14	1952	**
(16) Katire	15	1	7	25	6	24	40	7	17	1952	**
(16) Gilo	4	0	0	34	14	41	38	14	37	1952	**
Total	386	33	8.5	280	64	22.9	666	97	14.5		

* Serum retested at NAMRU-3 and found positive
** Tests made at Virus Research Institute, Entebbe, Uganda
† Tests made at NAMRU-3

black, and during the dry season becomes brick-like in hardness, with wide intervening crevices.

The Nuba Mountains are of volcanic formation and consist of a series of beehive-like rock masses rising abruptly from the plains and interspersed with valleys. Only the western range of these mountains was visited.

Climate

The climate is conditioned more by the rainfall than by the declination of the sun. The rainfall throughout the area visited is sharply seasonal. To the north in the region of El Nahud the annual rainfall does not exceed 13 inches (33 cm) and occurs mainly during the summer months, with only scant showers during the spring and autumn, and none whatever during the winter months.

Southward, the rainfall increases, and in the region of Wau may exceed 40 inches (102 cm). It also extends over a longer period but there are at least between three and four months with scarcely any precipitation. Consequently, throughout the area the ground and the vegetation becomes completely dry and parched except near the infrequent depressions (wadi) where the accumulated water remains during most, if not all, of the dry season.

The temperature during the day ranges from 90° to 110°F (approximately 32°-43°C) but it is usually comfortably cool at night.

Flora and fauna

The flora varies with the rainfall and the level of the land. In the vicinity of El Obeid and El Nahud, where the annual rainfall is only 13 inches (33 cm) the arboreal growth is sparse, consisting principally of stunted acacia with an occasional " tebeldi " (baobab) tree; the grass is also short. Around depressions, however, where water is retained during part of the dry season, the arboreal growth is more abundant and may include a few broad-leaf trees. Further south, the trees become larger and broad-leaf species are more common, but, with the exception of the region of depressions and along seasonal water-ways, the growth is largely of the orchard type—separated bush or stunted trees rather than a continuous or canopy forest. Southward, the grass becomes more rank, and south of the Bahr el 'Arab river, where large swampy areas are encountered, the " elephant " type, which reaches a height of 8-10 feet (2.5-3 m), prevails. During the dry season it becomes completely parched and dies, and it is the custom of the natives to burn it off in sections.

Only a very small proportion of the land is cultivated, mainly near the permanent villages and in a few isolated areas where the soil is suitable for the cultivation of cotton.

At one time nearly all the area was " big-game " country, but now the edible species have been largely eliminated and only south of the Bahr el 'Arab are antelope, giraffe, etc., commonly seen. The abundance of animals requiring a regular supply of water seems to be determined by two factors—first, available water during the dry season, and secondly, the density and the habits of the human population, who are their main pre-

dators. It is now essentially a grazing country, and the principal domesticated quadrupeds in order of importance are cattle, goats, and sheep. Birds of many species are common, and the swamps and rivers to the south are renowned for the variety and number of waterfowl.

Primates

Only four species of primate were observed. On the basis of observation and inquiry, the presence and prevalence of these four species are given in table II.

TABLE II. PREVALENCE OF PRIMATES IN SURVEY AREA

Species	Survey area		
	western border of Nuba Mountains	south-west plain north of Bahr el 'Arab river	south of Bahr el 'Arab river
Papio (baboon)	Present but scarce *	Absent or rare *	Frequent
Cercopithecus aethiops (grivet monkey)	Present but scarce *	Bands around widely-separate water-holes	Frequent
Erythrocebus patas (red hussar monkey)	Present but scarce	Present but scarce	Present but scarce
Galago senegalensis (bush-baby)	Spotty abundance	Spotty abundance	Spotty abundance

* None observed

During the dry season, the time that the visit was made, baboons and red hussar and grivet monkeys were observed only in the vicinity of surface water. The baboons and the red hussar monkeys may range during the day for some distance from the water source, but the grivet monkeys remain close by the broad-leaf trees which occur mainly around the wadis. North of the Bahr el 'Arab, the wadis where surface water remains throughout the dry season are few, and are commonly 10 miles or more apart.

On the other hand, the galagos were seen at considerable distances, probably far beyond their range of movement, from surface water, and it is presumed that they obtain sufficient moisture for survival from their food,

such as insects, worms, and buds and gum from bush and trees. Their presence seems to be determined by the character, density, and height of the arboreal growth. They were observed only in places where the trees were relatively high, 20 feet (6 m) or more, and sufficiently dense to permit the galagos to jump from one to another. Such areas are found mainly along dry stream-beds and in slight depressions. Here galagos may be quite abundant and as many as 20 were seen by night, by the light of a head-lamp, within an area of 10 acres (4 ha). Over large unfavourable areas, however, they were sought for in vain; hence the designation " spotty abundance " is used, although they are much more widely disseminated than the baboons and monkeys.

Obviously the notations on prevalence are only relative, but it can be said with reasonable assurance that, with the exception of galagos, the other species of primate are not sufficiently numerous north of the Bahr el 'Arab, nor in most of the Gogrial area south of the river, to account for the maintenance of yellow fever virus.

Population

Compared with western civilizations, and considering the potentialities of the soil, the human population over the great plains of the southern Sudan is sparse (no reliable statistics are available). Yet, because of the primitive methods of agriculture and animal husbandry, the standard of living is exceedingly low and food is scarce rather than abundant. The main problem is water during the dry season, and the people—whether permanent or nomadic—are clustered about water-holes and wells. In the Nuba Mountains, where water is available from springs, the population is more dense.

The plains-people north of the Bahr el 'Arab are usually called Arabs, and the Moslem religion prevails, but there is obviously a strong, if not predominating, mixture of negroid blood. The main industry is cattle-raising, and the rural population, which includes all except inhabitants of the larger villages and trading centres, are known as " Baggara " —cattle herders. Many of these people lead a nomadic existence, herding their cattle to available grass and water according to the season.

South of the Bahr el 'Arab river, the Dinker tribe of negroid Nilotic peoples is encountered; they also are largely cattle-raisers.

Collection of bloods

The collection of human bloods was necessarily selective. Some were collected in villages and should be more or less representative of the particular village; others were obtained at hospitals and dressing-stations, and represent a somewhat selective sample of the area served; and finally, samples were secured from schoolchildren drawn from the surrounding

territory. During the last visit covering the western and southern extension of the Nuba Mountains and the plains to the west and south, the great majority of the specimens came from schoolchildren below the age of 15 years.

For the collection of the primate bloods, the animals were generally shot and the blood drawn immediately from the heart or large blood vessel by means of a sterile syringe. A few of the galagos were captured and later chloroformed and bled from the heart.

For shooting the animals we had available a high-power .30-'06 calibre rifle, two .22 calibre rifles, and one each of 12-gauge, 16-gauge, and .410 calibre shot-guns. Experience demonstrated that while the .22 rifle was satisfactory for shooting grivet monkeys, the .30-'06 was far superior for killing baboons. The galagos were hunted at night by torch-light; a strong torch with not too narrow a beam is essential. The detached head-lamp of a jeep wired to a six-volt ("jeep") battery was found to be most useful; by having an extra battery, one could be kept constantly well-charged by using it in the "jeep" during the day. The larger-gauge shot-guns were first tried but were latterly abandoned in favour of the .410 calibre which is quite effective with No. 6 shot within a range of 30 yards (27.5 m). With the .410, the number of pellets which strike the animal are less than with the larger-gauge guns, and the chances of the heart and large arteries escaping injury and thus yielding a satisfactory blood-sample are greatly enhanced.

A thermos bottle with ice was carried and after the blood had been transferred into a rubber-stoppered tube of suitable size and allowed to clot, the tube was placed in the thermos. Upon return to the temporary base, the serum was separated from the clot by being spun in a centrifuge operated by a six-volt battery; it was then placed in a screw-capped vial. To avoid possible leakage the cap was secured by a band of adhesive tape. The vials were kept constantly iced during transport back to the laboratory at Cairo, where they were preserved at $-20^{\circ}C$ until examined.

Laboratory methods

Sera collected during the first two trips were sent to the Virus Research Institute at Entebbe, Uganda, for testing against yellow fever virus. The technique employed in examining these sera has been described by Smithburn.[10]

The sera collected during the last visit, which comprised most of the primate specimens, were examined at the United States Naval Medical Research Unit No. 3, Cairo (NAMRU-3). In this instance, the 17D strain was used and the inoculation of the serum-virus mixture was made intracerebrally into young adult mice, according to the method followed at the South African Institute for Medical Research, Johannesburg.

Briefly, the procedure was as follows. The virus suspension was prepared from the brains of mice inoculated with the 17D-vaccine virus, thus representing the first mouse passage of this attenuated strain. The serum-virus mixture was incubated for half an hour at 37°C before inoculation. Effort was made to use between 100 and 200 minimum lethal doses (MLD) of virus in the test; if, in a test run, the virus dose proved to be less than 100 MLD, all positive sera were retested with a larger dose of virus.

Six mice were inoculated with each serum-virus mixture. If all, or five of the six mice survived, the result was recorded as positive; if between two and four mice survived, the test was considered inconclusive; and if none or only one mouse survived, as negative.

Results of neutralization- or protection-tests

Human sera : Table I (see page 715) shows the results of yellow fever neutralization-tests performed on 666 sera collected in the Sudan during three excursions between November 1952 and March 1954. It is evident that the percentage of positive reactors is higher from Malakal southward than in places to the north of Malakal, and this applies to both age-groups. For example, the percentage of positives in the age-group below 15 years to the north of Malakal is 3, while from Malakal southward it is 15. Likewise, in the age-group of 15 years and over, the reactors are 8% and 30% respectively. These differences are significant. Exceptions to the rule occur mainly when the numbers involved are small.

As one of the main objects of the human blood collections in 1954 was to ascertain if yellow fever was still occurring in the Nuba Mountains area, the four positive tests encountered among children in Tukma, Um Dorein, and Talodi, all in the foot-hills of the Nuba Mountains, are of special interest. Two of these children were 12, and two were 13 years of age. If these tests are valid, and if the age given is correct, it is obvious that they were infected after the epidemic of 1940. In regard to their validity, it will be noted that no reactors among children were found further to the north at El Nahud and Abu Zabad. The other three localities sampled in the Nuba Mountains—namely, Kasha, Salara, and Kadugli—are somewhat further on the western edge of the mountains. We have no explanation for the immunity of one child (aged 12) found in a suburb of Khartoum, as it has not been possible to trace his previous movements.

It is not surprising that, among 35 sera collected from children at El Muglad, two positive sera were found, for, as will be referred to later, most of the grivet monkeys shot in this area were positive.

Primate sera : The primate sera comprised 56 galagos, 32 grivet and 2 red hussar monkeys, and 20 baboons. The results of the neutralization-

tests are shown in table III. Tabulation has been made according to the species of primate and the area where it was shot or captured. The inconclusive tests have been listed, as it was thought that they might be of some significance; they are not included, however, in calculating the percentage of positives.

TABLE III. RESULTS OF YELLOW FEVER NEUTRALIZATION TESTS ON PRIMATE SERA OF THE SUDAN

Map reference	Species	Total tested	Positive		Inconclusive **
			number	% **	
(4) Dilling	Galago	16	0	0	0
(5) Kadugli	Galago	12	0	0	2
	Red hussar	1	0	0	—
(6) El Muglad	Red hussar	1	0	0	—
	Grivet	17	11	69	1
	Galago	10	0	0	1
(11) Gogrial area	Baboon *	20	16	94	3
	Grivet	15	12	86	1
	Galago	18	1	6	1
	Total	110	40	40	9

* Includes six baboon bloods collected in 1953 and tested at the Virus Research Institute, Entebbe, Uganda

** In calculating percentage of positives, inconclusives are not included.

It will be noted that only one of 56 galagos gave what was considered as a positive reaction; this animal was shot in the Gogrial area. Four gave an inconclusive reaction with a small dose of virus. The remainder were negative, although in both the El Muglad and Gogrial area a high percentage of the grivet monkeys or baboons were positive. The over-all percentage of positives among the grivet monkeys is 77 (69% in the El Muglad area and 86% in the Gogrial area); 94% of the baboons (all from the Gogrial area) were positive. The two red hussar monkeys, both quite young specimens approximately six months of age, were negative.

Discussion

The results of neutralization tests on human sera in conjunction with previous surveys imply that yellow fever is rather highly endemic in the Sudan south of the 10th parallel and west of the West Nile. It would

also appear that human infection is occurring, probably to a lesser extent, in the semi-arid plains west of the Nuba Mountains as far north as El Muglad, and continues to occur in the Nuba Mountains.

With the exception of the Nuba Mountains after the epidemic of 1940, the rates and age-distribution of immunity found in this and preceding surveys, as well as the dispersion of the human population, are not in keeping with urban or village man-mosquito-man transmission by a domiciliary vector. Hence the reason for suspecting some other dominant or ancillary cycle involving other vertebrate hosts. That grivet monkeys and baboons are involved is evidenced by the high rate of immunity among them. However, the paucity of these species, particularly north of the Bahr el 'Arab river, discounts any likelihood that they alone could be responsible for the persistence of the virus.

It was hoped that the answer might be found in the galago, as this is the only primate other than man sufficiently abundant to supply the essential vertebrate host quota. Bugher [2] when working in West Africa found that the same species of galago which occurs in the Sudan was readily susceptible to infection with yellow fever, circulated virus in rather high concentration, and developed neutralizing antibodies. However, none of 50 captured galagos was immune. Smithburn [11] found that *Galago crassicaudatus lasiotis*, the species occurring in Kenya, was even more susceptible, and that over half of those experimentally infected succumbed. He also reported that 9 (14.5%) of 66 captured in Kenya were immune. The field data from Kenya have been further expanded by Haddow [3] and confirm the presence of immune galagos (14% among 103 examined), while in the same region none among nine baboons, and less than 2% of 335 monkeys comprising several species, were immune.

The finding of only one of 56 galagos giving a definite immune reaction, combined with the 10 negatives recorded by Kirk & Haseeb,[6] implies that this animal is not an important host of yellow fever virus in the Sudan. The same might be concluded, on the basis of Bugher's experience, for West Africa. It would seem, therefore, that while the *Galago crassicaudatus lasiotis* may be the principal vertebrate host in Kenya, *Galago senegalensis* does not play a similar role in the Sudan and West Africa. Since both species are susceptible to experimental infection, the discrepancy in their involvement with the infection in nature in the Sudan and West Africa and in Kenya may be due to differences in the nature and ecology of the responsible vector.

If the species of galago native to the Sudan is not involved, then some other explanation must be sought for the persistence of the virus. The pattern of immunity in man is not indicative of a purely man-to-man transmission by a domiciliary mosquito vector, nor is the number of monkeys and baboons sufficient to support alone the continuation of the infection; however, it is conceivable that, with man, monkeys, and baboons serving conjointly

as vertebrate hosts, in combination with a mosquito vector that attacks all three, the cycle of the virus might be maintained. This concept is plausible only because of the climatic conditions, and the rather peculiar habits and movements of the people on the western plains. The long dry season drives the Baggara or herdsmen and the monkeys to the vicinity of water-holes and wadis—the only places where water is available, with the exception of the permanent towns and villages which obtain water from deep wells. The Baggara people lead a nomadic life wedded to their herds. The cattle are moved from place to place according to the most favourable pasturage and, in the dry season, to available water, finally moving north to market. Thus there is a seasonal shifting of the cattle, and along with them the Baggara tribes, who may have no permanent abode, living camped in the open near their herds, and in the dry season clustered about the wadis. It is conceivable, therefore, that with a shifting human population and with the bands of grivet monkeys around the wadis, the chain of yellow fever virus is kept intact or is being constantly replenished by migrant Baggara tribes from the forests further south, where conditions are more favourable to its permanent retention. This description and hypothesis applies to the plains west of the Nuba Mountains, where the presence of the virus, as shown by immune children, and particularly by the high rate of immunity among grivet monkeys (El Muglad area), is most difficult to explain.

Obviously, further investigation is required to prove or disprove this hypothesis. Future studies should be concentrated upon the Baggara tribes and the mosquito vectors around the wadis during the dry season. The human bloods included in this survey were taken from schoolchildren who, for the most part, lived in the permanent towns and villages. It should be of interest to ascertain the immunity rate among the Baggara people; if the postulates expressed are correct, it should be considerably higher than among the more fixed village population.

It should be emphasized that this hypothesis has been tendered largely because no other explanation seems to fit the circumstances, unless there be some other hitherto unsuspected vertebrate host. It should also be stated that the hypothesis may not apply to other parts of the Sudan—the Nuba Mountains, for example—where the same conditions do not prevail.

Little can be said concerning vectors, as no effort was made to collect mosquitos during our trip to this region. However, it may be stated that mosquitos were observed only in the vicinity of wadis containing water. Lewis [7] has reviewed the distribution of species of mosquito in the southern Sudan that are capable of transmitting yellow fever virus, but it is felt that further study is required on the mosquito fauna near the wadis containing water throughout the year, for it is only here that mosquitos are likely to survive actively so that the virus may be propagated during the long dry season.

ACKNOWLEDGEMENTS

It is a pleasure to record the kindness and co-operation of all the administrative and medical personnel encountered during the visits to the southern Sudan, and to acknowledge in particular the aid of the Provincial Health Officer of Kordafan Province, Dr. Ibrahim A. Hussein, in supplying a truck, and that of the Assistant Provincial Health Officer, Dr. Ahmed Bukhary, who accompanied and assisted us during a part of the overland journey in this province. Grateful acknowledgement is also made to the US Foreign Aid Organization of Egypt for the loan of a " jeep ". We are especially indebted to Mr. Tom W. Chorley, Tsetse Survey and Reclamation Officer, whose unstinted co-operation, knowledge, and ability as a hunter made possible the collection of animal specimens in the Gorial area, and to Mr. R. C. H. Sweeny for lending us his Sudanese helper, who proved to be most efficient in directing the capture of galagos in the neighbourhood of Kadugli.

Mr. Harry Hoogstraal, head of the Department of Zoology, United States Naval Medical Research Unit No. 3, Cairo, participated in the first two visits to the Sudan, and his knowledge of the country and the people was of great assistance in obtaining human blood specimens.

Finally we wish to express appreciation to Dr. A. J. Haddow, Director of the Virus Research Institute at Entebbe, Uganda, and his assistants for performing neutralization tests on a portion of the human bloods, and to Mr. J. R. Kingston, Mr. L. J. Reobber, and Mr. Rostom Bablanian for assisting in the neutralization tests at this (NAMRU-3) laboratory.

RÉSUMÉ

Les tests de neutralisation du virus amaril effectués au Soudan sur 666 échantillons de sérums humains indiquent que la fièvre jaune est toujours endémique au sud du 10e degré de latitude N, à la frontière sud-ouest des Nuba Mountains et dans les plaines à l'ouest de cette chaîne, jusqu'à El Muglad. Il ne semble pas que, dans cette région, la transmission se fasse d'homme à homme par l'intermédiaire d'un moustique. Au cours de la recherche des hôtes vertébrés éventuels, on a soumis 110 primates aux tests de neutralisation. Les résultats ont montré qu'il existe une proportion élevée d'animaux immuns parmi les babouins (94 %) et parmi les cercopithèques (77 %). Toutefois, ces animaux sont en si petit nombre, dans la région considérée, qu'ils ne peuvent guère jouer un rôle prépondérant dans le maintien de l'infection. Les galagos *(Galago senegalensis)*, soupçonnés de servir d'hôtes, ne sont immuns qu'en très faible proportion (1 animal sur 56). Contrairement à ce que l'on observe au Kenya, où les galagos sont les hôtes importants de la fièvre jaune, ils ne semblent pas devoir être pris en considération au Soudan. Il faut donc trouver un autre chaînon pour expliquer la persistance de l'infection. On peut imaginer que l'homme, le babouin et le cercopithèque sont les hôtes vertébrés et qu'ils sont tous trois piqués par un moustique qui assure la transmission du virus. Les conditions climatiques qui règnent dans la région étudiée rendent cette explication plausible. La saison sèche attire près des points d'eau non seulement les populations nomades conduisant leurs troupeaux, mais aussi les singes. Il est possible que le cycle de transmission soit entretenu grâce aux mouvements saisonniers de ces populations qui, des forêts méridionales où les conditions sont favorables à la persistance du virus amaril, se déplacent vers le nord et vont camper autour des points d'eau, rencontrant là des moustiques qui peuvent s'infecter par piqûre d'un porteur de virus, et des singes auxquels ce virus peut ensuite être transmis. Cette hypothèse s'appliquerait à l'étiologie de la fièvre jaune dans les plaines à l'ouest des Nuba Mountains, où l'immunité élevée constatée

chez les enfants et chez les singes est difficile à expliquer autrement, tant qu'un hôte vertébré jusqu'à maintenant insoupçonné n'a pas été découvert. Elle est à vérifier par des recherches précises autour des points d'eau, en saison sèche, et si elle se confirme elle n'aurait probablement pas de valeur pour d'autres régions du Soudan, où l'ensemble des conditions qui viennent d'être décrites n'est pas réuni.

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