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Survival of Female *Anopheles gambiae* Giles Through a 9-Month Dry Season in Sudan*

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The dry-season biology of a member of the Anopheles gambiae *complex (probably species B) was studied in 2 areas in the Khartoum region of Sudan. It was found that in the valley of the White Nile the species maintained itself by low-level breeding, as shown by the continuing presence of larvae, male mosquitos and parous females through the dry months (9 months in the year). In the scattered villages of arid areas situated more than 20 km from the Nile Valley, on the other hand, regular sampling through the cool dry and hot dry months of the year failed to detect any* An. gambiae *except nulliparous females. These were found in occupied huts, deserted huts, dry wells and animal burrows.*

The great majority of 213 females collected in the 11 dry months between November 1966 and December 1967 had fresh or older blood-meals but the abdomen was never found fully distended in the dry season. Examination of the ovaries showed that they did not develop beyond Christophers' stage II in the period from November to February, stage III in March and April, or beyond stage IV in May. But, in June and July stage IV and V ovaries predominated and few specimens remained in stage late-II.

It is inferred from these observations that the local population of An. gambiae *is highly adapted to survive in the adult stage through the severe drought and heat of the arid zone of Sudan. Some feeding activity continues but ovarian development is extremely retarded, and only one batch of eggs matures during the whole 9-month period. Evidence collected in the Nile Valley indicated that female* An. gambiae *in that area were not subjected to similar retardation of the ovarian cycle ; in fact, clear evidence was obtained there of continuous year-round breeding by the mosquito.*

In the semi-arid parts of the Sudan, as in the rest of the hot-dry savanna region of Africa, it has been supposed that *Anopheles gambiae* disappears during the dry months of the year and reappears soon after the first rains fall. Nevertheless, mesoendemicity of malaria has been observed in much of this region. The question has arisen as to how species of this complex are maintained during the dry months or whether the region is reinvaded from elsewhere during the rains. The object of this work has therefore been to investigate the dry-season biology of *An. gambiae* under the severe climatic conditions of northern Sudan. It is hoped that the solution of this problem may assist the organization of malaria eradication and control programmes and contribute to their success.

Very little is known about the mechanism by which *An. gambiae* recolonizes desert and dry-savanna zones. It does so with remarkable rapidity soon after the first rains that are heavy enough to leave static surface water. Many hypotheses have been proposed to explain this phenomenon, but they are conflicting (de Meillon, 1947; Gillies, 1961, and personal communication 1966; Gillies & de Meillon, 1968). The studies reported here, which were the subject of a preliminary note (Omer & Cloudsley-Thompson, 1968), appear to go some way towards resolving this problem as regards one species—probably species B, according to Davidson's [3] distribution records of the complex.

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[3] Davidson, G. (1966, 1967) *Distribution records of member species of the* Anopheles gambiae *complex.* (Unpublished: Progress reports no. 11, 12, 13 and 15, Ross Institute of Hygiene, London, England).

THE STUDY AREA

The arid area investigated lies to the south-west of Omdurman town (Fig. 1). During up to 8 months of each year, there is no surface water in this region, or at any rate none that lies long enough to permit the production of mosquitos.

The region is a vast plain with small localized undulations. It slopes gently from west to east. The surface is broken by a number of *jebels* (hills), and dissected by several *wadis* (wide drainage courses) and *khors* (smaller water runnels). Stony areas appear here and there. East of longitude 32°0′ E runs a very large *quoz* (sand dune) known as Quoz Abu Dulu.

The *wadis* and *khors* which traverse this semi-desert country are lines of surface drainage in which rainwater accumulates as a result of run-off from the adjacent country during heavy downpours. Water only remains from a few hours to a few days after the rain (Halwagy, 1961) before it soaks away through the loose, unconsolidated material of the watercourses.

The study area lies within the region of the dry tropics, known as the *Acacia* desert-scrub (Andrews, 1948) or, as the " *Acacia tortilis–Meerua crassifolia* desert scrub " subdivision, of Harrison & Jackson (1958). Warm dry winters and hot rainy summers are characteristic of this semi-desert area.

Table 1, extracted from the records of the Sudan Meteorological Service, 1937–67, summarizes the climatic characteristics of Khartoum district. May is the hottest month of the year. The mean daily maximum temperature is 41.2°C in May and 41.0°C in June, while the mean daily minimum temperatures for these months are 25.8°C and 26.0°C respectively.

FIG. 1

WHITE NILE VALLEY SOUTH OF KHARTOUM AND THE ARID AREAS OF FATTASHA AND SUROBIT

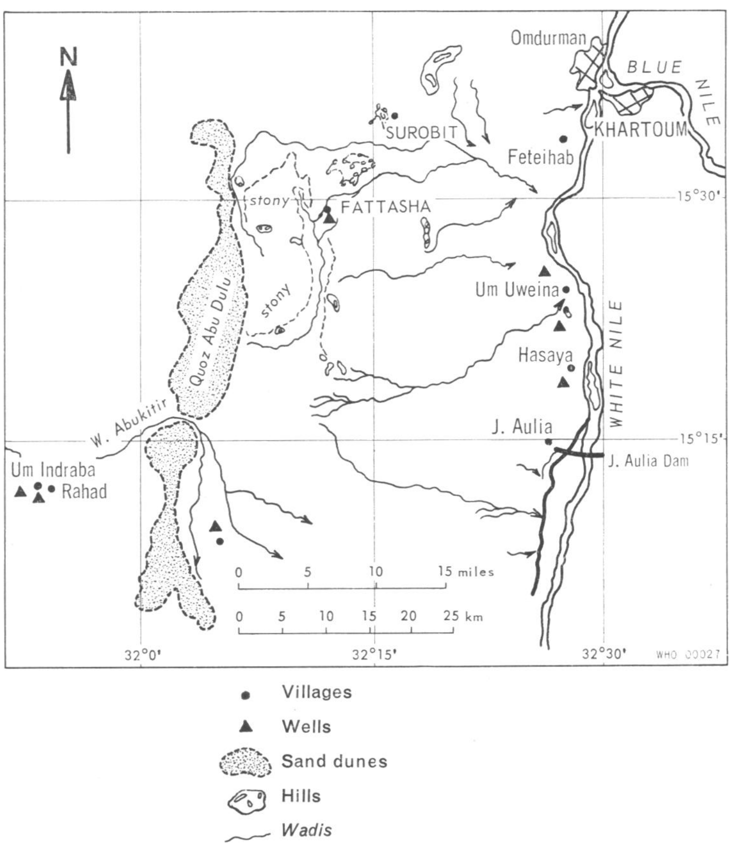


TABLE 1

MEAN MONTHLY CLIMATIC INDICES FOR THE KHARTOUM DISTRICT (1937–67)

Month	Mean daily maximum temperature (°C)	Mean daily minimum temperature (°C)	Rainfall (mm)	Percentage relative humidity at 08.00 h	Percentage relative humidity at 14.00 h	Percentage relative humidity at 20.00 h	Mean daily Piche evaporation (mm)
January	31.5	15.5	0	37	19	26	13.5
February	32.9	15.8	0	29	14	20	15.3
March	36.6	18.8	Trace	21	10	15	18.3
April	39.9	22.6	Trace	17	8	14	20.4
May	41.2	25.8	4.7	25	13	20	18.9
June	41.0	26.0	9.2	35	16	24	18.4
July	37.6	25.1	67.0	58	30	42	14.0
August	35.7	24.1	80.2	69	39	55	10.5
September	38.1	24.9	18.3	55	29	39	13.2
October	38.8	24.7	4.9	36	18	28	15.3
November	34.0	20.2	0	31	17	27	14.7
December	32.2	16.5	0	31	19	28	13.0
Annual mean or total	36.6	21.7	184.3	37	19	28	15.5

There are 6 rainless months from November to April. The mean annual rainfall is about 180 mm and about 95% of this total falls between July and October. The monthly distribution of the rainfall in 1966–67 is shown in Fig. 2.

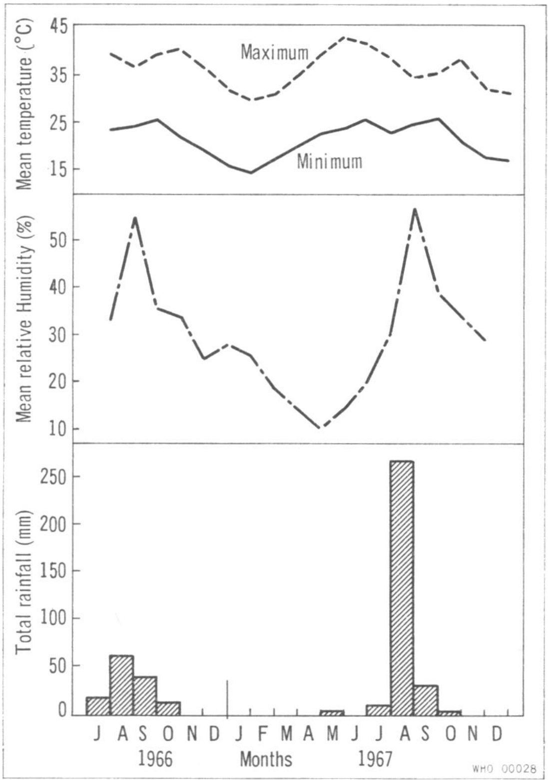
The winds blow mainly from 2 directions. The northerlies dominate from October to early May: during the winter season they bring cool dry air, but in April and May they carry intense heat from the Sahara Desert and Arabia, occasionally inducing sand or dust storms. In May the direction of the wind changes suddenly to the south: from May to July these southerly winds often cause violent sand and dust storms known as *haboob*.

The villages are scattered over the whole plain and are usually situated on high ground devoid of perennial vegetation, often in the shelter of a *jebel*. They tend to be scattered because the local population depends upon the grazing of the domestic animals and is therefore semi-nomadic. Villages are usually sited near places where rainwater remains for some time after the rains and where the wells do not have to be deep. The number of huts per village is small. Rain ponds and *haffirs* (man-made ponds) are utilized during and after the rain until the end of November. Wells are thereafter used as sources of water. Frequently these wells dry up towards the end of the dry season. The inhabitants of the village then move to another locality, usually not far from their homes. Such movements are generally reduced where there are deep pump wells from which water can be taken throughout the year. In such cases, people usually drive their animals away for grazing and return to their villages at night.

Fattasha (Fig. 3) consists of a group of 15 small villages scattered over a radius of some 5 km. Most of the villages lie on the high ground between 2 *wadis*: near the centre is a group of about 130 shallow wells 5 m–6 m deep, a government pump well, a dressing station (health post), a boys' school, a few dwelling houses and a shop. The total population is about 1200, comprising some 200 families. Each family owns approximately 100 animals; about 20 cattle, 40 goats and a number of sheep. Goats and sheep are herded in thorn enclosures in front of the dwelling huts. These are built of dried sticks, mats and grass. The people sleep inside their huts throughout the year. There is a watering pond a few hundred metres from each village.

Um Indraba is a resting-station for large flocks of domestic animals coming from the western Sudan. About 3000 animals pass through it daily. The wells there are deep, and ponds (*haffirs*) are used during the rainy season.

FIG. 2
CLIMATIC DATA FOR FATTASHA, SUDAN, JULY 1966–DECEMBER 1967



METHODS

Low-level breeding by An. gambiae *in the arid area*

In order to check the possibility of low-level breeding, the wells were sampled for larvae at Fattasha and Surobit. Each well was sampled at least once a week. A dip-net method suggested by Zahar (personal communication) was first used. The net was modified to increase its efficiency in sampling, by increasing its diameter so that the whole surface of the water in the well was sampled in 3 or 4 dips. In order to obtain better control of the net, one of us climbed down into the wells with the aid of a rope running through a pulley and held by the local assistants.

Traps were also set for emerging mosquitos, especially from disused wells with water. During April, May and June 1967, wells were hired from the villagers. A total of 6 emergence traps was used at Fattasha, and 4 at Surobit. The traps had a steel framework measuring 75 cm × 75 cm × 75 cm with a deep cone on one side: the cone had an apical opening 10 cm in diameter. The top and sides and the cone were made of mosquito-netting. A gauze sleeve, fitted to one side, facilitated the collection of the trapped mosquitos. The space between the edge of the well and the trap was sealed with cloth and mud and efficient thorn enclosures were then erected to exclude domestic animals. The traps were left for at least a fortnight over each well and checked every morning for emerging mosquitos. Each well was used only once during the period.

Existence and composition of adult An. gambiae *during the dry season*

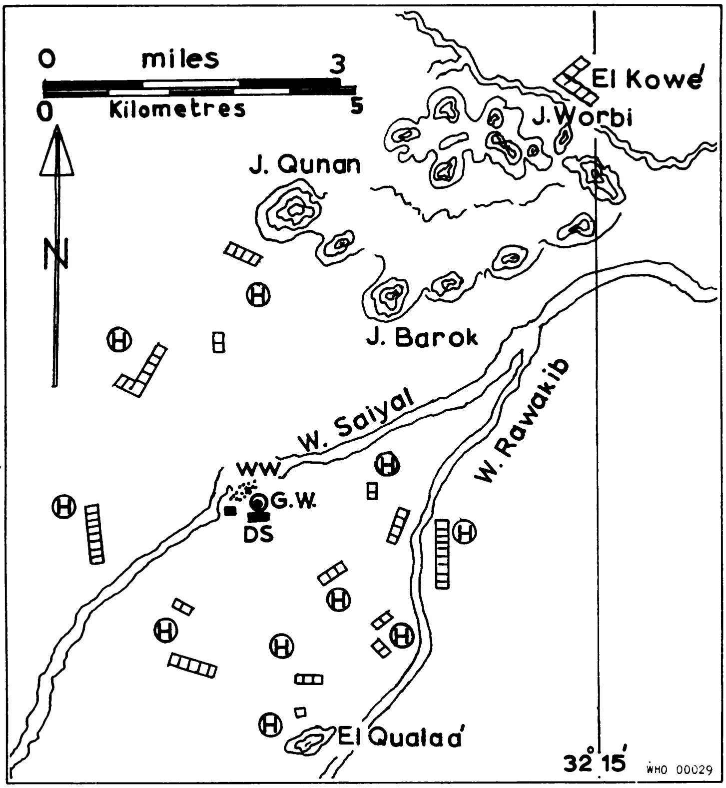
For pyrethrum-spray catches 0.3% pyrethrum in kerosene was used in 1-litre continuous sprayers. The floor and other horizontal surfaces inside the huts were covered with sheeting. Doors and cracks in the thatch were blocked before spraying. Spraying was carried out simultaneously from both inside and outside the huts. After 10 minutes the sheets inside the huts were checked by torch-light and specimens of *An. gambiae* were collected in tobacco tins lined with moist cotton, covered with filter-paper. The specimens were recorded and kept for dissection.

The search for adult mosquitos out of doors during the dry season was a time-consuming task. Cracks in the walls of the dry wells were examined by torch-light. When the cracks were too deep to be examined with a torch, a pyrethrum spray was used to induce any mosquito to come out. The roofs of rabbit and rodent burrows were carefully excavated with a shovel, and examined for resting mosquitos: fissures in trees and rocks, cracks and dark corners in ruined and disused houses as well as caves and rock shelters were also examined. Any mosquitos discovered in such sites were collected with an aspirator, transferred to labelled waxed-paper cups and kept for identification and dissection.

Well-traps similar to those used for emerging mosquitos were also placed over dry wells, with 2 sheep or goats tied near the thorn enclosure to serve as bait. The 6 traps employed in the region of Fattasha were checked every day.

Artificial breeding places were provided for the periods 2 January–21 February 1967 and 8 May–23 June 1967. In each village a large dish 45 cm in diameter, containing earth from *haffirs* and filled with water, was sunk in the ground between the door of a dwelling hut and the herd of domestic animals, when present. These dishes were kept filled by

FIG. 3
FATTASHA DISTRICT, SUDAN



WW Shallow wells
GW Government pump well
DS Dressing station
Group of dwelling huts
(H) *Haffir* (man-made pond)

means of a rubber tube from which water dripped continuously from a large container. Thorn enclosures were also erected so that animals could not drink from these dishes, and they were checked every fourth day for eggs and larvae.

Seasonal An. gambiae *densities along the White Nile and in the study area*

From November 1966 to December 1967 pyrethrum-spray catches were made on 1 day each month along the western bank of the White Nile at Feteihab, Um Uweina, Hasaya and Jebel Aulia villages (Fig. 1). About 5–7 houses were sprayed in each village, and the mosquitos collected were dissected to determine parity and ovarian development. Some wells were sampled for larvae using dip-nets. Larvae were also collected from water-holes, backwaters and from a reservoir, as well as from temporary surface waters during the rainy season.

Pyrethrum-spray catches were continued likewise at Fattasha during the rainy season on the same regular basis as during the dry season, and larvae were also collected from ponds, ditches, puddles, drains and other temporary surface waters.

RESULTS

Absence of low-level breeding in the dry season at Fattasha and Um Indraba

The dip-net sampling throughout the dry season gave negative results. Even climbing down into the wells did not reveal the presence of *An. gambiae*. Occasionally, *Culex* sp. larvae were encountered.

Trapping on the wells that contained water (in contrast to dry wells—see below) also produced negative results. No adult insect emerged, even when the traps were left in position over the wells for 3 weeks. Moreover, no aquatic stage of *An. gambiae* was found at any time in the breeding-pans set up at Fattasha. But on 1 August, only 5 days after the first heavy rain, a large ditch in this area was found to be teeming with second- and third-instar larvae of this species.

Existence of adults during the dry season

Pyrethrum-spray catches revealed that *An. gambiae* females were present throughout the dry season both in cool and hot weather. Table 2 summarizes the monthly catches in the area of Fattasha. The females killed were mostly found well away from the doors of the dwelling huts in dark places between the thatched roofs and the median longitudinal beams. At Um Indraba, the fallen mosquitos were found in the centres of those huts with conical roofs. Monthly catches in the dwelling huts of Um Indraba are given in Table 3. The tedious search for mosquitos in sites other than dwelling huts produced only 23 *An. gambiae*. Table 4 summarizes the results of this work at Fattasha and Um Indraba. The use of well-traps increased the numbers of females obtained from dry wells around Fattasha.

Alimentary condition and sources of blood

Of 115 females caught in the dry season in occupied huts in the Fattasha area (Table 2), 92 (80%) were found with blood meals. Of these 56 contained fresh blood and 36 contained old blood. Of 51 females caught at Um Indraba, 36 (71%) were found to have fed: of these, 21 contained fresh blood. The older blood meals were mostly dark in colour and very concentrated. Full distension of the mid-gut was not observed in freshly fed females. The feeding

TABLE 2

MONTHLY DRY-SEASON PYRETHRUM-SPRAY CATCHES OF FEMALE *AN. GAMBIAE* IN DWELLING HUTS AT FATTASHA (DESERT AREA): STATE OF STOMACH AND OVARIES

Month	No. caught	No. unfed	No. fed	Condition of blood (no.)		Christophers' stages of ovaries (no.)						
				Fresh	Old	I	II–E	II–L	III	IV	IV–V	V
1966												
November	17	5	12	8	4	10	7	—	—	—	—	—
December	19	2	17	10	7	12	6	1	—	—	—	—
1967												
January	18	3	15	12	3	5	9	4	—	—	—	—
February	8	2	6	3	3	1	4	3	—	—	—	—
March	10	4	6	4	2	—	2	7	1	—	—	—
April	8	—	8	6	2	—	1	6	1	—	—	—
May	9	2	7	3	4	—	—	3	5	1	—	—
June	10	2	8	4	4	—	—	1	5	2	1	1
July	16	3	13	6	7	—	—	—	1	8	4	3
Total	115	23	92	56	36	28	29	25	13	11	5	4

TABLE 3

MONTHLY DRY-SEASON PYRETHRUM-SPRAY CATCHES OF FEMALE *AN. GAMBIAE* IN DWELLING HUTS AT UM INDRABA (DESERT AREA): STATE OF STOMACH AND OVARIES

Month	No. caught	No. unfed	No. fed	Condition of blood (no.)		Christophers' stages of ovaries (no.)						
				Fresh	Old	I	II–E	II–L	III	IV	IV–V	V
1966												
November	9	3	6	2	4	5	3	1	—	—	—	—
December	6	1	5	3	2	3	3	—	—	—	—	—
1967												
January	7	1	6	5	1	2	4	1	—	—	—	—
February	6	2	4	2	2	2	2	1	1	—	—	—
March	6	1	5	3	2	1	2	2	1	—	—	—
April	5	2	3	2	1	—	2	2	1	—	—	—
May	1	1	—	—	—	—	—	—	1	—	—	—
June	4	2	2	2	—	—	—	1	1	1	1	—
July	7	2	5	2	3	—	—	—	1	3	2	1
Total	51	15	36	21	15	13	16	8	6	4	3	1

TABLE 4

DRY-SEASON CATCHES OF FEMALE *AN. GAMBIAE* FROM CRACKS DOWN DRY WELLS (W), RABBIT BURROWS (B) AND DISUSED AND RUINED HOUSES (H) IN THE STUDY AREA

Month	Fattasha						Um Indraba				
	Number caught/site [a]			No. fed	No. unfed	Ovarian stage (Christophers) [b]	Number caught/site [a]		No. fed	No. unfed	Ovarian stage (Christophers) [b]
	W	B	H				W	B			
Nov. 66	3 (1T)	—	—	—	3	I (II?)	—	—	—	—	—
Dec. 66	2 (1T)	—	—	1	1	II–E & II–L	—	—	—	—	—
Jan. 67	—	—	2	—	2	II–E & II–L	—	—	—	—	—
Feb. 67	2 (1T)	—	—	1	1	II–E	1 (T)	—	—	1	II–E
Mar. 67	1 (T)	—	—	1	—	II–L	—	—	—	—	—
Apr. 67	1 (T)	—	—	—	1	II–L	1	1	—	2	II–L & III
May 67	—	1	2	1	2	II–E, II–L & III	—	—	—	—	—
June 67	1 (T)	—	1	—	2	III & IV	—	—	—	—	—
July 67	3 (2T)	—	—	1	2	IV (2) & IV–V	1 (T)	—	—	1	III
Total	13	1	5	5	14		3	1	—	4	

[a] T = caught by well-traps.
[b] E = early; L = late.

TABLE 5

HUMAN BLOOD INDEX IN *AN. GAMBIAE* FEMALES CAUGHT IN HUTS DURING THE DRY SEASON AT THE STUDY AREA

Area	No. caught	Fed		Fed on human blood	
		No.	%	No.	% of no. fed
Fattasha	115	92	80	84	91
Um Indraba	51	36	71	32	89
Total	166	128	77	116	91

relations of *An. gambiae* caught in the study area rea summarized in Table 5.

In other resting places (Table 4) only 5 of the 23 mosquitos caught contained blood meals; precipitin tests showed that all were of non-human origin.

Ovarian condition and physiological age of An. gambiae *through the dry season*

The significant feature of the findings set out in Tables 2–4 is the very gradual advance of ovarian development shown by the surviving females as the dry season progresses. During the cool months (November–February) Christophers' stages II–III predominated, whereas stages IV–V were commonest in the following hot months (March–July).

The ovaries of all the 139 females collected in huts in the Fattasha area, in the 11 dry months between November 1966 and December 1967, were dissected to determine the proportion parous. Those in the early stages of development were examined for the uncoiling of the ovarian tracheoles, while the more developed ovaries were searched for the presence of follicular dilatations, for differences of colour in the ampullae and oviduct, and for retained mature eggs. Concurrent dissections of the same kind were carried out on samples collected in the White Nile valley.

TABLE 6

MONTHLY INDOOR CATCHES OF *AN. GAMBIAE* ALONG THE .WHITE NILE AND IN FATTASHA: PERCENTAGE OF FEMALES PAROUS

Month	Fattasha			While Nile		
	No. caught		% females parous	No. caught		% females parous
	Males	Females		Males	Females	
1966						
November	0	17	0	1	4	(75)
December	0	19	0	0	3	(33)
1967						
January	0	18	0	1	2	(50)
February	0	8	0	1	3	(67)
March	0	10	0	0	3	(33)
April	0	8	0	1	5	(60)
May	0	9	0	1	2	(100)
June	0	10	0	0	2	(50)
July	0	16	0	1	15	(40)
August	17	327	31	7	106	37
September	5	109	46	11	69	62
October	3	64	65	1	31	58
November	0	11	(10)	0	7	(28)
December	0	13	0	1	4 •	(25)

The results (Table 6) showed that (with a single exception in Novemter 1967) every female so captured at Fattasha in the dry months was nulliparous. Furthermore, no male *An. gambiae* could be found in those months. Along the White Nile, on the other hand, males were shown to be present in most months of the year and parous females were found in every month.

All the above findings tend to indicate that nulliparous *An. gambiae* survive through the dry season in the arid area, when no breeding is possible, in a state of reduced activity and greatly retarded ovarian development.

Analysis of dry-season catches along the White Nile

As shown in Table 6, sampling along the White Nile in the dry months produced a total catch of 58 *An. gambiae*: 8 males and 50 females. Dissection of the 39 females caught between November 1966 and July 1967 (Table 7) showed that in this area the earlier and later stages of ovarian development were not related to the advance of the season (as at Fattasha and Um Indraba), while 20 of these females, including at least 1 in every month, proved to be parous. Finally, inspections of artificial breeding-pans placed in the White Nile area showed that 3 pans were positive for *An. gambiae*: 2 had larvae and 1 had eggs. Natural breeding was confirmed by

FIG. 4

MONTHLY DISTRIBUTION OF THE TOTAL 14-MONTH CATCH OF *ANOPHELES GAMBIAE* IN 2 AREAS

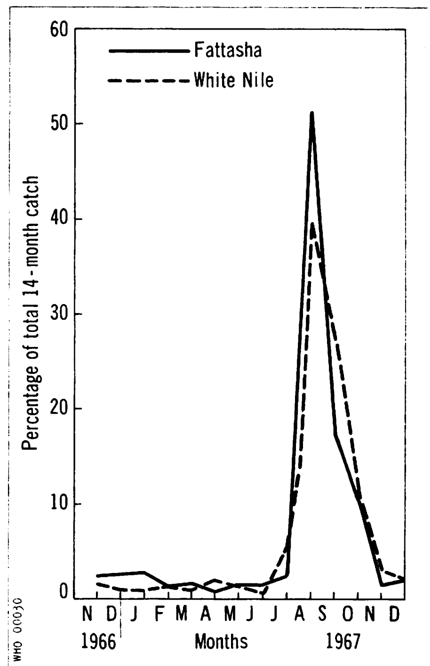


TABLE 7

OVARIAN STAGES OF FEMALE *AN. GAMBIAE* CAUGHT ALONG THE WHITE NILE DURING THE DRY SEASON

Month	No. caught	Christophers' stages of ovaries (no.)					
		II–E	II–L	III	IV	IV–V	V
1966							
November	4	—	1	1	—	1	1
December	3	—	—	1	—	1	—
1967							
January	2	—	—	1	—	—	1
February	3	1	—	—	1	—	1
March	3	—	1	1	1	—	—
April	5	1	—	2	—	—	2
May	2	—	—	1	—	1	—
June	2	—	1	—	1	—	—
July	15	1	3	5	2	1	3

the collection of larvae from backwaters, waterholes and from the reservoir of the Jebel Aulia dam: small numbers of *An. gambiae* were identified in November, February, March, May and June. Thus it is clear that low-level breeding continued uninterrupted in the White Nile valley, and no evidence was obtained there of seasonally arrested or retarded development in the adult mosquito.

The monthly proportions of the round-the-year catches of adult *An. gambiae* in the Fattasha and White Nile areas respectively are plotted in Fig. 4. Both populations maintained themselves at a low level during the dry season, and increased sharply soon after the rains began, although the mechanisms by which the 2 populations maintained themselves during the dry season were different. The seasonal decrease and increase in the White Nile population was slightly less sudden, probably because not all the females surviving at the beginning of the rains were ready to oviposit like those in the Fattasha area, while the temporary surface-waters suitable for breeding dried up less rapidly in the river valley than in the sandy desert of Fattasha.

DISCUSSION

A thorough survey of the study area in the desert west of Omdurman revealed that the only possible breeding places for mosquitos during the dry season were the wells. Seepages and other forms of permanent or semi-permanent surface waters were completely absent. Ponds and other waters present during the rainy season dried up somewhere between November and early January, the time depending on the amount of the previous rains.

Extensive sampling of the wells in the area of Fattasha and Surobit throughout the dry season failed to detect *An. gambiae* in these wells, although larvae of *Culex* sp. were occasionally encountered. The traps set over wells with water for periods of 3 weeks also gave negative results. *An. gambiae* males were never found anywhere in the area during the dry season although females were always present. This suggests that continued low-level breeding is not the mechanism by which *An. gambiae* survives the dry season in the study area. Low-level breeding of *An. gambiae* in shallow wells and underground water storage tanks has, however, been reported from northern Somalia (Choumara, 1961). In fact, the water in the wells of Fattasha and Surobit is not sufficient for the animal herds of the area. Each well is drained when the animals drink in the morning, and more water collects by the next morning. By early July (towards the end of the dry season), most of the wells contain no water at any time, and the villagers depend entirely on the government pump well for water.

Behavioural and physiological changes among the anopheline mosquitos of the temperate regions are primarily related to the cold season. Adult anophelines survive the winter in a state in which activity is arrested or greatly retarded. This inactivity may lead to full hibernation, the main vital activities being arrested, or to incomplete hibernation in which at least one form of physiological activity continues, even though it may be retarded. This form of diapause is distinct from quiescence, in which the inactivity is a direct response to some unfavourable condition of the environment (e.g., low temperature) and which ceases immediately the conditions improve (Andrewartha, 1952; Clements, 1963). In hot climates, the absence of, or irregularity of water for breeding, and the extreme atmospheric aridity emphasize the survival value of quiescence and aestivation (Bates, 1949; Andrewartha, 1952).

In different parts of the world many anophelines pass the unfavourable cold season as adults. Adult *An. labranchiae atroparvus* have been found hibernating in houses and stables in Europe. The insects took blood meals, but their ovaries did not develop (Swellengrebel, 1929). Roubaud (1932) described this lack of development rhythm as " gonotrophic dissociation ". Complete hibernation (in which both ovarian development and feeding activity cease) as well as partial hibernation (like that described by Roubaud) have been reported within the *An. maculipennis* group. Russian workers showed that gonotrophic dissociation, as well as gonotrophic concordance, occurs in *An. maculipennis messeae*. The adaptive incidence and intensity of diapause differs in different environments (Andrewartha, 1952).

Gonotrophic dissociation has been reported in anophelines in southern Asia. Strickland (1938) suspected that this phenomenon may occur in *An. maculatus* in eastern India. Afridi, Majid & Shah (1940) found no evidence of hibernation or gonotrophic dissociation in *An. culicifacies*. They stated that the activity of this species showed a gradual retardation from September to February, although pupae could be collected. Some individuals lived for an exceptionally long time during the cool dry season. It was concluded that *An. culicifacies* must be well adapted to withstand the inconstancy of its environment. Rao (1947) described what he called "gonotrophic discordance" in *An. culicifacies* and *An. annularis* in eastern India. In about 20% of the population the ovarian development of the females ceases, while feeding is repeated. Moreover, these individuals exhibit a suspension of sexual activity. He concluded that there is a certain degree of gonotrophic dissociation as well as of gonotrophic concordance within the same species. In other Indian species ovarian development may take longer than the normal period and is dependent on repeated feeding. Büttiker (1958) observed a physiological state which he termed "partial quiescence", in *An. culicifacies* and *An. aconitus* of Burma and Ceylon. During the beginning of the dry season he found the mosquitos with coagulated, dark red and almost desiccated mid-gut contents. He found no signs of ovarian development, nor did he observe any fat reserves. He suggested that the aestivating females might maintain themselves throughout the dry season on the last blood meal, but that they might occasionally come out of their shelters to take water in the form of dew.

Little is known about the seasonal physiological changes in anopheline mosquitos in Africa. Aestivating female *An. funestus* have been found in Southern Rhodesia, hiding deep among the rocks in the beds of rivers during the dry season. The females, which were in a state of torpor, contained almost completely developed ovaries during the cool dry season (Leeson, 1931). When the temperature rose they left their shelters, oviposited and died soon afterwards. De Meillon (1934) has reported a condition resembling hibernation in *An. gambiae* in South Africa. He found adult females, which took frequent blood meals, resting under stones during the dry season. In a personal communication (1967) de Meillon suggests that the resting adults he observed may well have represented species C, the zoophilic, exophilic member of the *An. gambiae* species complex now recognized. Holstein (1954) found female *An. gambiae* passing the dry season in dwelling huts, ruined or uninhabited huts, holes in rocks and cracks in soil, covered pigsties, rabbit hutches, hen coops, cattle pens and dry wells, at Bobo-Dioulasso, Upper Volta. These females contained completely developed ovaries and were able to feed whenever the opportunity arose. Fat reserves were not found, and Holstein concluded that what he had observed was a state half way between gonotrophic dissociation and gonotrophic concordance. Females kept in the laboratory, under conditions approximating to those in nature, lived for periods up to 156 days, during which time they laid eggs 2–3 times. Holstein also noticed that the longevity was much greater at low than at high humidities (112 days at 35% R.H. and 27°C; 87 days at 63% R.H. and 29.5°C). Individuals deprived of sugar and blood survived starvation for as long as 70 days. He suggested that fasting females probably maintain themselves on the nutrition provided by their own eggs.

Lewis (1956) found *An. gambiae* in the Gezira area of the Sudan hiding in earth cracks during the dry season. Our present observations in the arid area of Sudan confirm that *An. gambiae* females were present throughout the dry season. All those taken during the dry season were nulliparous, and although artificial breeding places were provided, no oviposition took place. Of these females, 77% contained blood. It should be noted that no plant juices are available during the long dry season, since none of the sparse vegetation in the desert region blossoms during that period. These findings lead us to think that *An. gambiae* in the study area must exhibit a degree of arrested ovarian development. The nulliparous females complete only 1 gonotrophic cycle during the long dry season (November to July inclusive).

We consider that long-range flights are unlikely to be the mechanism by which the species reinvades the arid area. Such flights, though known in *An. pharoensis* (Garrett-Jones, 1962), have not been reported for *An. gambiae*. The maximum flights reported are around 6.5 km to and from breeding places (de Meillon, 1934; Gillies, 1957, 1961). Gillies (1961), using the mark-and-release method in the coastal region of Tanzania, showed that *An. gambiae* dispersed to a maximum of 3.6 km with a marked reduction in the numbers recaptured at this distance. True migratory behaviour has not, to our knowledge, ever been recorded in this group. The south wind prevailing in the area before and during the rains appears to exclude the possibility of passive dispersal by wind.

Our observations on wild-caught females were supported by laboratory experiments in which females were kept in a cool, dry environment. Some were reluctant to feed, but could survive starvation for 59 days. In others the taking of blood meals was coupled with an almost complete cessation of ovarian development. This is not typical gonotrophic dissociation or gonotrophic concordance as described in other anophelines, but it is more like the former. It seems to be an incomplete form of ovarian diapause. It may well be an adaptation of the species to withstand the climatic extremes of its environment.

Owing to its dry season biology *An. gambiae* may be capable of transmitting malaria all round the year in the arid parts of Sudan. This is seen in records that indicate malaria transmission throughout the year.

RÉSUMÉ

SURVIE D'*ANOPHELES GAMBIAE* GILES FEMELLE PENDANT 9 MOIS DE SAISON SÈCHE AU SOUDAN

La biologie d'un moustique du complexe *Anopheles gambiae* (probablement de l'espèce B) durant la saison sèche a été étudiée dans deux zones de la région de Khartoum au Soudan. Dans la vallée du Nil blanc, la présence continue de larves, de moustiques mâles et de femelles pares pendant les mois secs a permis de conclure que l'espèce se maintenait grâce à une reproduction faiblement active. Par contre, dans les villages dispersés des zones arides situées à plus de 20 km de la vallée du Nil, les échantillonnages régulièrement faits au cours des mois frais et des mois chauds de la saison sèche n'ont permis de détecter aucun *An. gambiae* à part des femelles nullipares. Celles-ci ont été trouvées dans les huttes occupées ou désertes, des puits à sec et des terriers.

La grande majorité des 213 femelles récoltées avaient fait plus ou moins récemment un repas de sang. Toutefois, on n'a jamais observé pendant la saison sèche de femelles complètement gorgées. L'examen des ovaires a montré que ceux-ci ne s'étaient pas développés au-delà du stade II de Christophers de novembre à février, au-delà du stade III en mars et avril, ni au-delà du stade IV en mai. En juin et juillet, on a observé surtout des ovaires complètement développés ayant atteint les stades IV et V et dans un très petit nombre de cas seulement des ovaires à la fin du stade II.

On conclut de ces observations que, dans la zone aride du Soudan, la souche locale d'*An. gambiae* est bien adaptée pour survivre, au stade adulte, pendant la sécheresse et la chaleur intenses de la saison sèche. Les moustiques continuent à s'alimenter quelque peu, mais le développement ovarien est extrêmement retardé, une seule ponte parvenant à maturité pendant toute la période. Dans la vallée du Nil, on n'a recueilli aucune indication permettant de penser que les femelles d'*An. gambiae* soient sujettes, dans cette région, à un retard similaire du cycle ovarien; en fait, les observations ont nettement démontré que le moustique peut s'y reproduire en toute saison.

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