INVESTIGATIONS INTO THE BIONOMICS OF *GLOSSINA PALPALIS*.

By W F. Fiske.

Introduction and General Discussion.

These studies were made in Uganda on the islands and shores of Victoria Nyanza, in territory which had been depopulated some years before on account of tsetse-fly and sleeping sickness. They were begun in October 1913, and extended over two full years, of which eighteen months were spent in the fly belt on Victoria Nyanza, and three months on a tour into Bunyoro, where for the time being (the spring of 1914) *Glossina morsitans* was the centre of greater attraction as a possible vector of human trypanosomiasis. Seven tours were made from headquarters at Entebbe—the shortest, of three days only, being interrupted by the War, and the longest, of eight full months, being much prolonged by the War.

The working basis unquestioningly accepted in the beginning was that the measures adopted in 1906–07 for the suppression of sleeping sickness in Uganda were both wise and necessary. These measures called for complete severance of contact between the fly and the native populations so long as infection was present. They had contemplated originally the elimination of infection through complete severance of contact between fly and population, but in this particular had failed of their object, for the trypanosome persisted both within and without the depopulated zone; as a parasite of game and fly within it, and as a human parasite in the riparian populations of adjoining sectors of the lake region without it. They therefore required the extermination of fly in populated districts, or as a prerequisite to reclamation and repopulation of territory from which the inhabitants had been removed. They were exactly such measures as are absolutely required for suppression and prevention of the cattle trypanosomiasis transmitted by *Glossina morsitans* in other parts of Uganda; and going on the perfectly natural assumption that a close parallel existed between human and bovine trypanosomiasis, as transmitted by *Glossina palpalis* and *Glossina morsitans*, respectively, the wisdom and necessity of the measures was not questioned.

The economic or practical objective of the studies was the sanitation and reclamation of the fly-infested territory; the more immediate and technical objective, therefore (proceeding on the above assumption), was the extermination of fly as a sanitary prerequisite to reclamation. To exterminate a species is to restrict its range or distribution. Therefore, the most immediate objective was made that of identifying and studying those factors in the bionomics or "control" of the species which operate in nature, or which might be operated by artifice, to delimit and determine or to "control" its range.

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It was an integral and most important feature of the original plan that, after the factors which operate in the "natural control" of the insect should have been identified and studied, an experiment should be conducted on a "practical" scale to demonstrate at the same time the accuracy and the economic applicability of the knowledge acquired. By the spring of 1915 sufficiently definite conclusions had been reached on the particular points at issue to justify this experiment. Until then the investigations had been conducted on the islands. The experiment could not be made on the islands, but must be made on the mainland. Consultation with the Principal Medical Officer as to the best site for it led to the selection of the Buddu district, which borders the lake for some ninety miles just north of the old German frontier. Therefore a tour was made with the object of surveying this reach of shore carefully, to ascertain the degree of infestation by the tsetse; the probable cost of exterminating it; the precise location of old village sites, canoe landings, fishing grounds, etc., with respect to fly; and such other points as required consideration preliminary to any experiment of the character proposed.

The results of this survey were unexpected, and led to a complete revolution of ideas previously entertained. The reach of shore is naturally divided into a considerable number of semi-isolated districts, having from two and a half to seventeen miles of frontage on the lake. Some of these districts were found to be infested by tsetse to a degree of density never before encountered. Others were very lightly infested. In one district a few days labour with a good gang of men would have sufficed to exterminate all the fly on a reach of some five miles. In this case the natives would very willingly have given the labour in return for the lands and the fishing grounds off shore, for the lands were good and extensive and the fishing grounds productive. In several other districts it was thought probable that the value of the land and water rights was sufficient to induce the natives to undertake all the labour requisite to exterminate fly without other expense to the Government than that of supervision and inspection. Any of these would have been an excellent site for the proposed experiment.

There was one district, however, Bukakata, which had a frontage of some six and a half miles on the lake and included the steamer landing for Masaka station, that presented a strange problem. The lands adjoining the lake in the depopulated or forbidden zone were valueless for agriculture. The fishing rights were valuable, and would have been a considerable inducement to the natives to clear the shore of tsetse, except for the fact that the natives were already occupying them, openly, for the entire reach of six miles. Infestation by tsetse was much heavier than in certain other districts, but still moderate, exceeding the average for the lake shore and islands as a whole at only a few points, and averaging for the district about half the average for the region generally. Careful inquiry failed to elicit a particle of evidence that any of the native fishermen had suffered in the slightest degree from long-continued exposure to tsetse under these conditions.

At certain other points along the shore surveyed poaching was free and flagrant; at one point in particular, where density of fly was more than seven times greater than the average for the region generally, and where, in addition to this, food (of fly) was very scarce and the flies literally ravenous, twenty-three fish traps, some new and some old and discarded, were found along a two-mile reach of shore, indicating regular and long-continued contact between trespassers and fly at its very worst. Less aggravated conditions were frequently encountered along many reaches of mainland shore.

On returning to Entebbe a special survey was made for fly within the inhabited precincts and for trespassing by natives beyond them. It was found that a considerable portion of the township was very lightly, but constantly or regularly, infested by fly (to an easily measurable degree), and that at certain points in the environs natives went freely into contact with fly at a moderate—but nowhere excessive—degree of density. Similar conditions prevailed at Jinja and at Kampala, the two other lake ports.

With these conditions in mind, inquiry was made concerning the number of cases of sleeping sickness recorded in the official death returns or coming to the attention of Medical Officers; for it was thought certain that some must occur. To my very great surprise I learned that, so far as known, not a single case had been contracted within the Province of Buganda—for which the returns are most reliable—since 1912, and that with the exception of two cases (one of them not surely trypanosomiasis, and the other possibly contracted in Busoga) among the men who accompanied Dr. G. D. H. Carpenter on his tour to the islands in 1911–12, no cases were known or suspected to have been contracted since the islands were depopulated in 1909.

A curious situation was thus created, which led to the abandonment of the proposed experiment and to complete readjustment of ideas and preconceptions. In theory—the theory upon which the suppressive and preventive measures had been based—complete severance of contact between fly and population was necessary in order to control sleeping sickness, but in actual practice complete severance of contact was found to be unnecessary. In theory it was necessary either to exterminate fly from populated districts or to make removal of inhabitants "from the vicinity of tsetse complete and without exception"; but in practice it was proved sufficient to reduce the density of fly to within moderate limits in populated districts or to reduce density of population to within moderate limits in fly-infested territory.

If this is really sufficient, knowledge concerning factors which control range of the insect is more or less superfluous, whereas knowledge of factors which operate to control breadth of contact between fly and population—equivalent to frequency of contact between hungry flies and men—is specifically required.

Two very different lines of study are thus outlined. Which of them ought to be followed?

As a matter of fact, both were followed: the first up to 1915, and the second during the last months of field work. One of them was impractical, and the specific results of it are practically valueless, except as disjointed fragments of information gained can be salvaged for use in other connexions. Which of these two lines of investigation ought to be reported upon?

In the accompanying manuscript neither has been reported upon, because this question has not been answered, nor any specific object for the preparation of any report defined. It contains a mere mass of unapplied, and for the present inapplicable, information of no practical value until a decision has been reached on the following points :—

(1) Shall the original plan for these investigations be followed, and an experiment be planned and conducted to test the accuracy and applicability of the conclusions reached ?

(2) If so, shall the object be—

(*a*) to exterminate fly and prevent all contact between fly and population, in accordance with the theories held in 1906–07 ; or

(*b*) to reduce excessive density of fly and to prevent excessive breadth of contact between fly and population, in accordance with present practice —as in the Bukakata District in 1915–16 ?

Unfortunately the decision cannot rest on the results of these studies in tsetse bionomics, which have only the most indirect bearing upon the point at issue. Every bit of information which seemed, even remotely, to bear upon them, and which could be gleaned from any available source, was included in a report presented in 1916, upon which no action has been taken at this date of writing. The one phase of tsetse bionomics having any bearing on these points is the fly's choice of hosts and host preferences. This is enlarged upon in the following pages.

The methods used in conducting these studies consisted in the main of a " fly survey " of the lake shore and islands. This survey was designed to measure as accurately as possible all peculiarities and variations in the range of the insect, and all variations in its density as they occurred from time to time in the same localities, or from one locality to another at the same time. Coincidently observations were made and notes kept concerning every factor known or suspected to operate in the " natural control " of range and density, with the object of identifying those of major importance, *i.e.*, such as are responsible for easily measurable peculiarities in range or variations in density. No attempt was made to study specific factors—such as natural enemies—unless they were indicated to be of sufficient importance to account for measurable variations in density. By this procedure much useless work was avoided.

These methods were especially applicable to studies having as their ultimate or practical objective the extermination of the insect. But after the readjustment of old ideas and preconceptions of the economic problem, made necessary by the discovery that it is practically unnecessary, and even, for economic reasons, undesirable to undertake extermination of fly, entirely different methods of study were demanded. The questions to be answered involved less the range and density of tsetse and the factors controlling them than the injuriousness of the tsetse and the factors in its control. The injuriousness of the insect, or its injurious status in relation to a population occupying the same or adjoining territory, is, in part, but only in relatively small part, determined by density of infestation. Factors of equal or even greater importance are those which control the frequency of contact between flies and persons, and these include the relative abundance of host animals (such as crocodiles), the principal occupations of the population, the precise location of points of occupation or concourse of the population with respect to colony centres of fly, and various others to which the original fly surveys had accorded only incidental attention or had left out of consideration entirely. Reduction in density of fly is one object; reduction in the injuriousness or injurious status of fly is, in actuality, a totally different object, and methods of study must vary accordingly.

Finally, it was disclosed that the question of paramount importance was one that required yet different methods of study. It is to define the extent to which frequency of contact between flies and persons inhabiting a given region must be reduced in order to bring human trypanosomiasis under effective and satisfactory control. It is a question which can only be answered by measuring the frequency of contact and the coincidence of trypanosome infection in the population. It is, I regret to say, impossible for me to carry on investigations along this most necessary line unaided. It is for the entomologist to measure density of fly and frequency of contact between flies and men, and to identify and study the factors in control, but unless he is specifically trained to diagnose and detect trypanosome infection, his studies are incomplete and of relatively little value.

Every effort was made in 1915 to secure the co-operation of a Medical Officer for a tour along the coast and islands of Nyanza Province (British East Africa), where the riparian populations had not been removed; but, on account of the War, nothing could be done. Some little information on this point was gleaned from old (manuscript) reports of Medical Officers employed on "Sleeping Sickness Extended Investigations" in Uganda, which, as far as it went, strongly confirmed the presumption that the disease is incapable of spreading unless there is excessive breadth of contact between fly and population—in excess, for example, of that encountered in the survey of the Buddu shore in the Bukakata District—and a few other scraps of information have been found in literature—for example, in Todd and Wolbach's survey for human trypanosomiasis in the Gambia, which contains a few brief references to prevailing density of fly and frequency of contact—but it is a line of investigation which has yet to be systematically followed.

I. Disparity between the Sexes of Glossina palpalis.

When any considerable number of flies of this species of *Glossina* are caught, it is unusual to find the sexes evenly represented. Although they are produced in equal or approximately equal numbers, they are caught in unequal numbers.*

This disparity between the sexes of *Glossina palpalis* is an extremely variable quantity, ranging in different localities (in catches of 100 flies or more) from 1·9 per cent. to 85·0 per cent. of females or from 15·0 per cent. to 98·1 per cent. of males. Females never predominate to quite the extent of males, and most frequently the males are in excess.

Various hypothetical explanations for this phenomenon have been proposed by Medical Officers and Entomologists who have observed it, and prior to the inception of these investigations all these explanations presupposed that "caught flies are hungry flies" (attracted to their captor through desire to feed on his person), therefore

* "Thus of 1,400 flies bred from pupae obtained on Damba Island the proportions were ♂ : ♀ :: 48 : 52. Whereas of 5,000 flies caught during the period in which the pupae were collected the proportions were ♂ : ♀ :: 78·6 : 21·4." Carpenter: Repts. of the S.S.Comm. of the Royal Soc., xii, p. 105.

that the ratio between the sexes in the catch would be an index to the ratio actually existing between all flies in the locality or district where the catch was made. The deduction is logical from every point of view

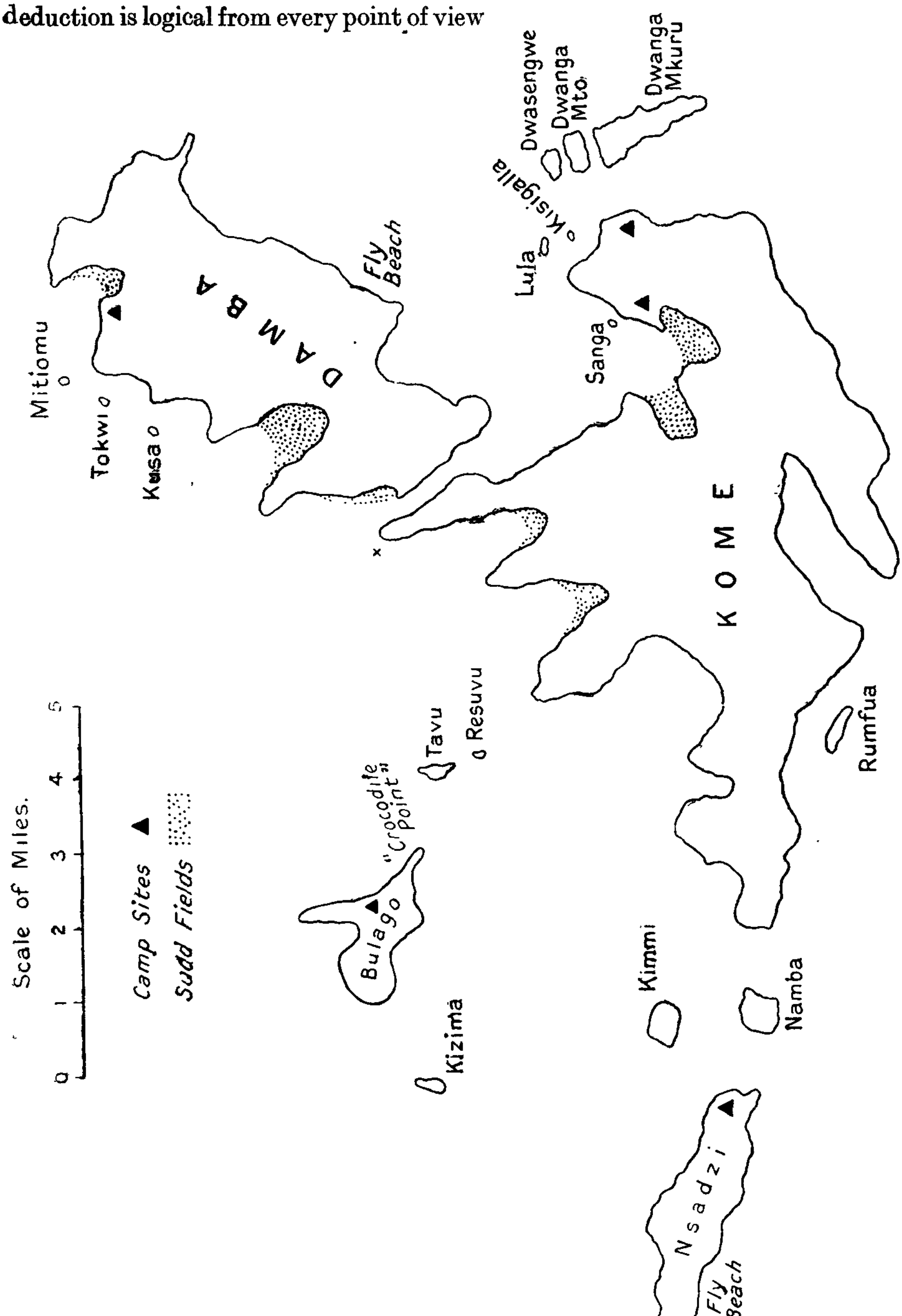

Fig. 1. Sketch-map of the Kome-Damba Group of the Sesse Islands.

But what becomes of the surplus males in localities where females predominate, or of surplus females, when, as usually is the case, males predominate, were questions that had not been answered when these investigations were begun. Whatever the explanation might be, it was certain to be intimately involved with phases in the bionomics of tsetse the nature of which could only be guessed, but the importance of which could not be doubted.

A minor problem was thus defined which served as a starting point for further investigations into the broad and complicated subject of the bionomics of *Glossina palpalis*, and the first field-work done was the series of experiments an account of which follows.

I(*a*). Experiment to determine if Variations in Sex Ratio of *Glossina palpalis* are due to differences in the purely local, or in the climatic or seasonal Conditions of Life.

The Islands of Bulago and Tavu (fig. 1) are separated by only a few thousand yards. Tavu is much the smaller and differs also in topography and vegetation. But the two islands are so near together that any difference in sex ratio, if constant and if occurring at the same seasons of the year, would necessarily be due to purely local conditions.

Large collections of fly were made on the two islands as shown in Table I. There was considerable variation in sex ratio observed on Bulago on different days (when collections were made at different points on the island), but in the total catch of 4,405 flies there were proportionately twice as many females as in the total catch of 3,126 flies from Tavu. This difference could only be attributed to purely local differences in conditions of life between these two islands.

TABLE I.

Catch of Fly from Bulago and Tavu Islands, showing relatively constant difference in Sex Ratio.

1913.	Island.	Daily Catch.		Total Catch.	
		Total.	Females.	Total.	Females.
1st Nov. ..	Bulago ..	170	35 %	170	35 %
2nd " ..	" ..	18	17 %	188	33 %
3rd " ..	" ..	60	24 %	248	32 %
4th " ..	" ..	630	25 %	878	28 %
5th " ..	" ..	564	27 %	1442	27 %
6th " ..	" ..	656	18 %	2098	25 %
10th " ..	" ..	651	20 %	2749	24 %
11th " ..	" ..	1057	27 %	3803	24·5 %
12th " ..	" ..	167	18 %	3970	24 %
13th " ..	" ..	435	29 %	4405	25 %
5th " ..	Tavu ..	136	4 %	136	4 %
6th " ..	" ..	1179	8·3 %	1315	7·8 %
7th " ..	" ..	945	18 %	2260	12 %
8th " ..	" ..	866	13 %	3126	12·4 %

Much wider variations in sex ratio between different islands were subsequently noted, and the extremes are given in Table II. In all such cases—or at least in most of them—explanations for variations in sex ratio must be found in the purely local conditions of life, and not in climatic or seasonal differences.

The absolute extremes encountered in the course of the investigations, together with the records for all colonies of fly or infected districts in which female percentage exceeded 45·0 are presented in Tables III and IV.

TABLE II.

Extreme Range in Variation of Sex Ratio (observed) between different Islands in Victoria Nyanza.

Island.	Date.	Catch of Fly.	
		Total.	Females.
Kimmi	January 1914	7065	63·5 %
Luambu	July 1915	557	44·3 %
Wema	February 1914	1413	39·1 %
Bugovu	March 1915	415	39·0 %
Ngamba	January 1914	761	7·9 %
Bugabu	August 1914	704	7·9 %
Mbugwe	September 1914	73	4·1 %
Nkase	February 1915	101	3·0 %

TABLE III.

Absolute Extremes in Sex Ratio as encountered in course of these Investigations on Islands and Mainland.

Locality.	Date.	Catch.	Per cent. Fem.	Remarks.
Manene Island..	March 1915..	46	0·0	Largest catch with no females.
Bugaba Beach ..	August 1914..	106	1·9	Lowest percentage of females in catch of over 100 flies.
Manene Island..	March 1915..	107	1·9	(same as above)
Bukakata ..	July 1915..	30	90·0	Largest percentage of females in catch of over 10 flies.
Bale Beach ..	June 1915..	241	84·6	Largest percentage of females in catch of over 100 flies

TABLE IV.

Catch in those Districts on Mainland where Female Percentage averaged 45·0 *or over for entire District.*

District.	Date.	Catch.	Percentage of Females.
Mujuzi Creek Colony, Buddu	June 1915..	1611	67·6
Bukakata South Colony, Buddu	July 1915..	298	51·0
Kaziru District, Buddu	July 1915..	991	50·6
Kitebo District, Mawakotu	August 1915..	1199	47·5
Gwamba District, South Buddu	July 1915..	3422	45·0

I(*b*). Relative Inactivity of Females of *Glossina palpalis* as the Explanation of Low Female Percentage in Catch.

The figures of the catches of fly from Bulago and Tavu Islands presented in Table I show a discrepancy in that the percentage of females in the total catch from Bulago Island tended to fall as the total grew, whereas on Tavu it rose sharply. This might be accidental, but the circumstances under which the experiment was conducted indicated otherwise. Tavu Island is much smaller than Bulago, and the catching of some 1,300 flies on the 5th and 6th of November seemed to have reduced the local density of the species appreciably, as measured by the average number of flies which could be caught per boy per hour. A corps of 9 or 10 boys was employed. During these first days of the investigations the exact time spent in catching was not recorded. It was approximately known, however, and when the catch of males and females per boy per hour (approximately) is tabulated it stands as in Table V.

TABLE V.

Reduction in Density of Glossina palpalis *on Tavu Island due to catching of Fly.*

1913.	Catch of Fly.		"Boy Hours."	Density of Fly Indicated.		
	Males.	Females.		Males.	Females.	Total.
6th November ..	1081	98	36	30·0	2·7	32·7
7th ,, ..	734	169	45	16·3	3·7	20·0
8th ,, ..	698	111	45	15·1	2·5	17·6

TABLE VI.

Catch of Glossina palpalis *on Lula Islet, showing the relative Inactivity of Females.*

Period (November 1913).	Catch for Period.			Catch to end of Period.	
	Males.	Fe-males.	Female Ratio.	Total.	Females.
18th Afternoon	280	18	6·0 %	298	6·0 %
19th Morning	308	72	19·0 %	678	13·3 %
19th Afternoon	93	68	42·2 %	839	18·8 %
20th Morning	83	146	64·3 %	1068	28·5 %
20th Afternoon	36	89	71·2 %	1193	32·9 %
21st All Day	95	224	70·2 %	1512	40·8 %
22nd ,, ...	51	79	60·8 %	1642	42·4 %
24th ,, ...	29*	73	71·5 %	1744	43·5 %
25th ,, ...	28*	93	76·9 %	1865	46·2 %
26th ,, ...	29*	65	69·1 %	1959	47·3 %
27th Morning	17	53	75·7 %	2029	48·3 %

* These figures, apparently, represent about the daily emergence of males from pupae; all the old flies of this sex appear to have been caught off.

These data indicate that whereas the density of male flies had been reduced from 30·0 caught per boy per hour on the 6th to 15·1 on the 8th, that of female flies had not been appreciably reduced—exactly as though the females were actually present on the island but for some reason not so easily caught as either (*a*) the males on the same island, or (*b*) the females on Bulago Island (Table I).

This hypothetical explanation for a low percentage of females in the catch suggested the experiment of catching all the flies from an islet. Tavu was rather larger than convenient and the yet smaller islet of Lula (Fig. I) with an area of hardly more than 10,000 square yards was selected.

The results of this experiment are presented in Table VI. It was not carried to a final conclusion because of the time which would be required to catch all the flies emerging from pupae on the island (at least three weeks longer than the period devoted to it), but it was carried far enough to demonstrate conclusively that a very low percentage of females may be due to the relative inactivity, and not, as had always been assumed, to the absence of the sex.

I (*c*). The Percentage of Females among caught Flies as an Index to Food Supply.

An analysis of the data presented (in part) in Table VI and secured during the course of the Lula experiment above described disclosed the curious fact that although the catch of males fell sharply from 14·0 per boy per hour on the the first day to 2·6 and 1·7 on the morning and afternoon of the third day (see Table VII); that of females rose strikingly from ·9 per boy per hour on the first to 4·5 and 4·4 on the morning and afternoon of the third day. Otherwise stated, the density of active male flies was quickly and permanently reduced to one-eighth or less of the original, but that of active female flies actually increased by no less than five times during the same period that that of the males was being reduced by seven-eighths.

TABLE VII.

Analysis of Catch of Fly made on Lula Islet showing Variation in Activity of Females.

Period (November 1913).	Density* of Active Flies.		
	Males.	Females.	Total.
18th Afternoon	14·0	·9	14·9
19th Morning	9·7	2·2	11·9
19th Afternoon	3·5	2·8	6·3
20th Morning	2·6	4·5	7·1
20th Afternoon	1·7	4·4	6·1
21st All Day	1·8	4 1	5·9
22nd ,,	1·0	1·6	2·6
24th ,,	·7	1·7	2·4
25th ,,	·9	2·9	3·8
26th ,,	·7	1·4	2·1
27th Morning	·6	1·6	2·2

* By "density" is meant the number of flies which can be caught per boy per hour.

This strange increase in the activity of the female flies on this islet was obviously associated with the experiment being conducted there, and that which seemed the most plausible explanation was that the male flies are normally active and easily caught at all times during good weather, whether they are hungry or not, but that the females are normally inactive and not to be caught except when hungry and seeking food. This hypothesis was borne out by the observation (made during the course of the experiment) that the mere presence of the corps of fly boys (9 or 10 of them) on the islet had temporarily banished from it the several crocodiles and *Varanus* which had formerly frequented it and which were the only visible sources of food for the flies. Assuming that only hungry females are active and easily caught, the effect of this would be to increase the number of them and therefore the number caught per boy per hour, through decreasing their food supply.

On this hypothesis such variations in the percentage of females amongst caught flies as are presented in Tables I and II (*i.e.*, such as occur between different islands) would indicate corresponding variations in abundance of food, or density of host animals. It was resolved to test this hypothesis by banishing the host animals from a small islet without catching off any of the flies, and observing the effect on sex ratio.

This experiment was made on the small island of Lugazi, in the following manner and with the following results.

19th and 20th December 1913. A total of 197 flies were caught on the islet, the sex was determined and they were then liberated (in order that catching off of males should not affect the sex ratio). The ratio was, males : females : : 166 : 31 = 15·5 per cent. females.

22nd to 27th December 1913. All host animals known to be fed upon by *Glossina*, consisting of several *Varanus* and crocodiles, were systematically hunted from the islet.

26th and 27th December 1913. A total of 208 flies were caught, showing sex ratio, males : females : : 89 : 119 = 57·2 per cent. females.

This experiment was carefully conducted, and careful notes were kept upon the behaviour of the flies on the islet towards man and also towards certain domestic animals which were tethered there (see Sect. II (*b*)). They were so strikingly affected by the banishment of their reptilian hosts as to leave no doubt that they had been principally dependent on them, and that the increase in percentage of females from 15·5 to 57·2 was the direct result of food shortage. Data on this phase of the experiment appear in Sect. II following.

I (*d*). The Real Ratio between the Sexes of *Glossina palpalis*.

The foregoing observations and experiments demonstrate conclusively enough that the ratio between the sexes of caught flies is no criterion of the real sex ratio in the locality where the catch is made. It would be impossible to determine the real ratio accurately, otherwise than by the continuation of such an experiment as was made on Lula until all flies had been caught, and this would require more time than the knowledge is likely to be worth.

It is believed, however, that the ratio in the catch on Lugazi after the hosts had been banished from the island (57·2 per cent. of females) is not far from representing the real ratio between the sexes on that particular islet. The more active males pretty certainly run greater risks, and do not on the average live so long as the less active females, and the real sex ratio would be determined by respective longevity of the sexes—probably a variable quantity.

An explanation is thus provided for any ratio between the sexes of caught flies from, say, 60 per cent. to 70 per cent. of females down, but doubtfully for female percentages of 70, 80 or even 90, such as are occasionally encountered. The explanation for these excessively high percentages was a mystery until long after the conclusion of the Lugazi experiment, when investigations into the movements of flies along the shore of a lake or stream provided the explanation (see Sect. III) and at the same time additional confirmation of the conclusions, tentatively reached through the Lugazi experiment, that the percentage of females in caught flies may serve as an index to the abundance of food (or density of host-animals) in the region where the catch is made. This conclusion is undoubtedly correct, provided that the catch is truly representative of the district or region; it is not correct if the catch is made under specific conditions (with respect to shelter, etc.) described in Sect. III.

II. The Variable Behaviour of Glossina palpalis towards Man and Domestic Animals as correlated with Variations in Sex Ratio.

The conclusions tentatively reached through the foregoing experiments are of interest in a vital connection. They suggest that if the female percentage is low, food must be plentiful, and man would be less liable to attack. Moreover, when a great majority of the flies are feeding regularly on reptilian hosts—which do not carry the virus of the human disease—many flies, or a dense infestation by fly, would be less injurious to man and less liable to transmit disease from man to man than if there were only a few flies, or a light infestation, feeding principally or exclusively on man, or on animals which may carry the virus of human disease.

Therefore, if the conclusions are correct, the injuriousness of *Glossina palpalis* to a population living in constant contact with it would be subject to variations independently of any variations in density of the fly, or of any other factor than the abundance of host animals incapable of harbouring the virus of human disease, and if it were attempted to reduce the density of fly, with the object of minimising its injuriousness, through measures directed against its host animals, the results might be the opposite of those desired. Through a campaign of extermination directed against its reptilian host, its density might be reduced, but its injuriousness increased.

Several experiments were conducted and many observations were made which have a bearing on the point, and which were also designed to confirm the conclusions to the Lula and Lugazi experiments cited above; for if these conclusions are correct, there must be a conspicuous correlation between variations in female percentage and in the persistency with which tsetse-flies press their attacks upon man.

In part, these experiments and observations are cited in this immediate connection (as confirmatory of the preceding conclusion); but they are further cited in subsequent pages in other connections.

II (*a*). **Methods used for Estimating the Density and Economic Status of** *Glossina palpalis.*

The most convenient method for measuring variations in the density of *Glossina palpalis* is that of employing expert "fly boys" and of counting the number of flies which can be caught per boy per hour under standardised conditions. This method had already been used by Dr. G. D. H. Carpenter and others, and when care was taken to eliminate sources of error very reliable figures were secured.*

On account of the very variable activity of the females it is obvious that estimates of local density must be based on the catch of males. That of females is of little significance by itself in indicating density, but taken in connection with the catch of males it possesses a large significance, and is indicative of variations in the economic status of the fly. This, like density, varies extremely (*a*) from time to time in the same region or locality, and (*b*) from one district or locality to another at the same time. It is in part determined by the density of fly, and variations in density correspond to variations in economic status (*i.e.*, by reducing density we assume that we depreciate the injurious status of the insect, and its status must naturally vary with natural fluctuations in density); but in larger part it is determined by the behaviour of the fly towards man, and this in turn by abundance of wild hosts. The female percentage is an index to abundance of hosts, and therefore to the liability of man to attack.

To illustrate the above, two extremes cited in Table III may be used: the infestations as measured in Bugaba and Bale beaches respectively. In each case the actual catches of fly were made at three points a few hundred yards apart on these beaches, and the complete data concerning degree of infestation are presented in Table VIII.

At first glance, in comparing the density of fly at these two points on the basis of the total catch—both sexes—per boy per hour, it would appear that there were twice as many flies along the Bale as along the Bugaba beach, for the total catch is more than twice as great. But the difference is very largely due to the enormously greater activity of the females at Bale, and if allowance is made for as many, proportionately to the males, at Bugaba as at Bale, it appears that there are almost three times as many fly at Bugaba, instead of less than half as many.

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* Proper attention to the following suggestions will serve to eliminate various possibilities of error :—

(1) Boys should be trained at least one month; all new boys in a corps without one or or two experts as teachers would require longer training.

(2) Nets must have a standard-sized ring and a standard length of handle; an 8-inch ring and 18-inch handle were used.

(3) Catches should not be made before 8.30 or 9 a.m. nor later than 2.30 or 3 p.m.

(4) Boys will make more even catches if provided each with a dark-coloured umbrella, upon which the flies will settle, and from which they are easily caught.

(5) Unless density is very low—less than 1·0—it is better not to spend more than 2 to 3 "boy hours" at the same point on the same day; density is easily reduced, temporarily, by catching.

(6) Boys should be stationed along the routes most likely to be followed by moving flies, and always, if there is shadow, at the edge of it.

(7) Estimates of density must be based on catch of males, on account of the variability of female activity.

(8) Good results cannot be secured on cool, cloudy or windy days.

TABLE VIII.

Extremes of Variations in Economic Status of Glossina palpalis *as indicated by Female Percentage.*

Locality and Point.	Catch of Fly.			No. of "Boy Hours."	Indicated Density.			Female Ratio.
	Males.	Fe-males.	Total.		Males.	Females	Total.	
Bugaba – Pt. 15..	33	1	34	3	11 0	·3	11·3	3·0 %
" 16..	39	1	40	1½	26·0	·6	26·6	2·5 %
" 17..	32	0	32	1½	21·3	·0	21·3	·0 %
Bale—Pt. 49 ..	20	84	104	2	10·0	42·0	52·0	80 8 %
" 50 ..	10	80	90	2	5·0	40·0	45·0	88·8 %
51 ..	7	40	47	2	3·5	20·0	23·5	85·1 %
Totals—Bugaba..	104	2	106	6	17·3	·3	17 7	1 9 %
Bale ..	37	204	241	6	6·2	34·0	40·2	84·6 %

It is also necessary to take account of the reason for the excessive activity of female flies at Bale. If this is caused by scarcity of food, it appears that all the females, and obviously the males as well, must be hunting for food. Therefore a man fishing on the beach would be likely to encounter no less than 40 hungry flies per hour.

But at Bugaba there would be only one hungry female each three hours, and if the males are proportionately hungry, not more than two flies that were actively seeking food would be encountered each three hours by the fisherman. This would indicate that the fisherman on Bale beach would be exposed to 60 food-hunting flies to 1 for the fisherman at Bugaba; *i.e.*, the fly at Bale, though less numerous by half, is indicated to be 60-fold more dangerous to a population living in contact with it than the fly at Bugaba.

This point seemed so important that confirmation of conclusions tentatively deduced by the above method was sought in various ways, and the final conclusions are that the fly really varies in economic status over a much wider range than as above indicated. There are several reasons for making this the final conclusion which need not be gone into; the point upon which evidence is submitted in the pages immediately following is that of the much greater freedom with which fly attacks man when the female percentage (for a district or region) is high than when it is low.

II (*b*). Correlation between High Percentage of Females, artificially produced, and Persistence of Attack upon Man.

In the course of the Lugazi experiment to which reference has already been made (p. 357), two adult goats and one—subsequently another—small pig (of European stock) were tethered, equally exposed to attack by *Glossina*, along the shores of the island. From the 15th to the 20th of December great care was taken not to disturb the wild hosts of the fly on this islet. The female percentage taken on the 19th and 20th was found to be 15·5, which was probably maintained throughout this period.

From the 22nd December the wild hosts (crocodile and *Varanus*) were systematically hunted from the island. The effect on the behaviour of fly toward the tethered host animals was not noticeable on the first day, but appeared on the second in the increased number engorging upon them. The third day was overcast and flies were inactive, but on the fourth day, as may be seen from Table IX, a very notable increase in the number of flies engorging was brought about.

The percentage of females was determined anew on the 26th and 27th, and was found to have increased from 15·5 to 57·2. This was certainly due to decrease in number of wild hosts; the increase in number of flies engorging upon domestic animals was certainly due to the same cause, and is thus directly correlated with variations in sex ratio.

TABLE IX.

Showing Effect of hunting Wild Hosts from Lugazi Islet upon Behaviour of Glossina palpalis *toward Goat and Pig.*

Conditions on Islet.	Date (1913).	Pig.			Goat.		
		Hours exposed.	Flies engorging.	Bites per Hour.	Hours exposed.	Flies engorging.	Bites per Hour.
Wild hosts undisturbed. Female ratio 15·5 %.	15th December	—	—	—	9½	—	—
	16th ,,	—	—	—	2	—	—
	17th ,,	4	—	—	8	—	—
	18th ,,	3¾	—	—	7½	—	—
	19th ,,	8	1	·12	16	—	—
	20th ,,	8	—	—	16	—	—
Wild hosts hunted. Female ratio increasing to 57·2 %.	22nd ,,	8½	—	—	17	—	—
	23rd ,,	18	5	·28	18	3	·17
	24th ,,	17	4	·24	17	2	·12
	25th ,,	18	49	2·72	18	6	·33

The behaviour of fly toward man underwent a change quite as striking as in its behaviour toward pig. At first it was attempted to keep an exact record of the number of flies attacking the observer and the fly boys. From the 15th to the 20th inclusive only one fly bit and none engorged upon the observer. The fly boys were equally immune. During this period no one paid any attention to the fly nor was any effort required to ward it off.

On the 22nd December no difference was noted and no flies bit the observer.

On the 23rd "Flies were more active than I have seen them." Four flies bit the observer.

The 24th was a dull day. "Flies very inactive but bothersome. Four flies bit; others would have bitten if permitted to do so." The fly boys were equally annoyed, and considerable effort was required to keep flies at a distance.

On the 25th it was necessary to be constantly on guard against the flies. "The flies are hungry—very hungry. They attack man viciously, and it is impossible to estimate the number of times I have been bitten or would have been bitten but for constant vigilance. All the fly boys were on the *qui vive*, and continually fighting off flies, in sharp contrast to complete indifference toward them on the 22nd and previously."

Undoubtedly more flies would have bitten man on the 25th than actually engorged upon the pigs that day, and their changed behaviour toward man was equally as notable as shown by the table (IX) toward pig.

This experiment of hunting the wild hosts of tsetse was accidentally repeated on the peninsula of Neozi on the island of Bugalla (Sesse) where camp was pitched in November 1914. There was a not heavy or noticeable infestation by tsetse, and the principle host of it was situtunga. But no sooner was the camp occupied than these animals evacuated the peninsula and were seen crossing the isthmus connecting it with the mainland one to two miles distant only a few hours after the men began work on the tent and huts. On the following day (Sunday) the behaviour of the flies was not notably changed, but on the third day they became so unbearably persistent in their attack that (in view of the possibility of human infection from their bites) the camp was abandoned.

Such conditions are likely to be produced in almost any fly-infested locality by the advent of a temporary population sufficiently large to produce a measurable effect upon host animals. They are particularly likely to be created when, as was formerly a custom of the natives, temporary fishing camps are located on small islets which are otherwise uninhabited. If a person infected by the human parasite is a member of such a fishing party conditions will be extremely favourable to the transmission of the organism to other members of the expedition.

II (*c*). **Correlation between High Percentage of Females naturally prevailing and Persistence of Attack upon Man.**

The islands listed in Table X were visited in January and February 1914 in company with Dr. Carpenter. Large collections of fly were made and the average of male density and of female percentage recorded for the several observation points on each island is also given in the table. Dr. Carpenter and I were agreed, at the close of the tour, that the relative persistency of attack by fly upon man was fairly estimated as in the table.

The difference between behaviour of fly towards man on Kimmi and Damba, respectively, was truly extraordinary—equally as extraordinary as its changed behaviour on Lugazi islet following the banishment of its wild hosts. And these differences are strikingly correlated with variations in sex ratio, and not at all, or only as by accident, with variations in density of infestation (as measured by density of active males).

These observations have been many times confirmed, notably by the behaviour of flies on Bale fly beach (Table VIII), where the female percentage was 84·6, and where, despite constant vigilance, the observer was actually bitten about 15 times per hour. This is more times in one hour than he was bitten in more than six weeks spent in field work on the islands of Bulago, Kome, Damba, Tavu, Lula and others, from 1st November to 15th December 1913. A record was kept of the number of bites inflicted during this period and it totalled only 9. When the fly is no more troublesome than this, the ordinary person makes little effort to ward off attack, and nearly every fly that cares to bite does so, but when the fly is as troublesome as at Bale, where " nearly every fly tried to bite " the ordinary person is continually on the alert to ward them off, and not nearly so many flies bite as would otherwise do so. The difference in behaviour of fly towards man on such islands as Tavu, Bulago, etc., and on the fly beach at Bale is even greater than the figures given above would indicate.

TABLE X.

Correlation between Female Percentage and Behaviour of Glossina palpalis *towards Man.*

Island.	Catch.	Density*	Females.	Behaviour of fly towards man.
Kimmi ..	1588	24·3	57·5 %	More troublesome than on any other island.
Wema ..	1413	30·5	39·1 %	At times or in places as bad as on Kimmi but not always so bad.
Yempaita .	1382	42·6	37·9 %	About as bad as Wema would average.
Bulago ..	580	27·5	29·0 %	Not as bad as on preceding island, but bad enough.
Nsadzi ..	1080	18·4	24·6 %	Not as bad as Bulago, but worse than on Tavu at times.
Kizima ..	513	15·1	18·9 %	Not at all troublesome.
Tavu ..	674	46·6	17·1 %	Not as bad as on Bulago.
Damba ..	975	30·7	12·2 %	Less troublesome than on any other badly infested island.

* Owing to the varying degree of activity of females the density of fly in any district or island must be based, for comparative purposes, on the catch of males alone.

II (*d*). Experiment to test Variability in Behaviour of Fly towards Man on Kome or Damba Islands, as correlated with Variations in Abundance of Host Animals and Female Percentage.

In the autumn of 1915 a definite and detailed scheme was worked out for the reclamation of and re-establishment of the populations upon the Sesse Islands. One detail of this scheme was the placing of a colony on the island of Kome (Fig. I), which in itself is one of the safest in the lake and could easily be made much safer, but which suffered severely from sleeping sickness owing to the nearness of the island of Damba, which, when populated, was probably the most insanitary island in the Sesse group ; it must have been continuously much as Lugazi islet was after being occupied for three days by hunters of the wild nosts of tsetse. It would be entirely impractical to make Damba a safe place for a native population to live unless there were much more need for agricultural land than at present. But wild hosts were so numerous and female ratio so low that theoretically Damba, if unpopulated, and set aside as a bit of game reserve, would not be a source of danger to a population on Kome.

It was desired to test this theory by pitching camp on Kome, and spending some days hunting over and surveying both it and Damba, keeping accurate count of the number of times that flies actually bit—without engorging—during the days spent in the experiment. This was done; camp was pitched squarely in the fly belt on Kome; three days were spent in exploration and survey of bush and old plantations along its shore; four hunting trips were made to Damba, and afterwards two days were spent in a camp located squarely in the fly belt on that island.

The results of the experiment are summarised in Table XI. Host animals were more than five times as numerous on Damba as on Kome, with the result that female percentage was very much lower. Density was not less than six times greater on Damba, but owing to the relative scarcity of wild hosts, fly was much more prone to bite on Kome, when one-sixth the number of flies inflicted nine times as many bites. This would indicate the fly to be nine times more likely to transmit disease on Kome than on Damba, although the density is only one-sixth as great.

TABLE XI.

Comparison of the Behaviour of Glossina palpalis *towards Man on Kome and Damba Islands.*

Basis of Comparison.	Kome.	Damba.
Number of hours spent in bush along shore at times when fly was active	14	22
Number of hours spent in camp in fly belt, at times when fly was active	10	8
Average density of fly in bush, about	5·0	30·0*
Average density of fly at camp, about	5·0	15·0
Female percentage in bush	38·1	10·2
Wild hosts of fly seen or flushed:—		
Varanus	0	12
Situtunga	7	50
Total	7	62
Wild hosts seen or flushed per hour	0·5	2·8
Number of times observer was bitten in bush	3	0
,, ,, ,, camp	4	1
Total	7	1
Number of times bitten per hour in bush	0·21	0·0
,, ,, ,, camp	0·40	0·12
Number of times bitten per hour spent on island	0·28	0·03

* The catches made during this trip indicate a somewhat heavier infestation than this, but it is known that they were too high; they were made at points where flies were concentrated, and allowance is made for lower average density.

The really striking comparison, however, is between the figures as given for Damba, and the note made during field work on the beach at Bale (see p. 362) to the effect that "nearly every fly tried to bite," and that 15 actually bit in less than one hour.

Density, as indicated by the male catch at Damba, is three or six times greater than at Bale, but at Damba 22 hours were spent in the bush without being bitten once, as compared with 15 bites in one hour at Bale, a proportion of less than 1 to more than $15 \times 22 = 330$.

Making allowances for error at every point, it is clear that density of infestation being equal, the fly is several hundred times more likely to feed upon man where wild hosts are very few and female percentage very high than when they are very many and female percentage low.

II (*e*). **Female Percentage as an Index to the Chances favouring Transmission of Human Trypanosomiasis.**

Perhaps the most pertinent point in this connection is that the chances favouring transmission of the virus of sleeping sickness from man to man are vastly less proportionately when few flies feed on man than when many do so. The same fly must feed on or bite the human host twice in order to transmit disease from an infected to a healthy man. If only one fly in 500 or 1,000 actually bites man, the chances that that same fly will attack man a second time are absurdly small; if every second or third fly feeds upon or bites man the chances that the same fly will attack man a second time are stupendous in comparison.

The female percentage may thus be a very valuable index to the chances favouring transmission of human disease.

III. The Long-shore Movements of Glossina palpalis.

The explanation of the variable ratio between the sexes of *Glossina palpalis* provided by the early experiments proved inapplicable in many cases, and numerous vagaries in the sex ratio were observed which were for long inexplicable.

Eventually investigations into the long-shore movements of flies and the routes and courses followed by them in their food-hunting and otherwise stimulated flights, led back into the old problem of sex disparity and provided logical explanation for many variations in it which had been observed but which could not be correlated with abundance or scarcity of food. The same study also required consideration of "shelter" (arborescent vegetation sought or required by the flies for their protection) and of the relative attractiveness of different types of it.

These three, quite different topics—sex disparity, shelter, and movements of flies from place to place—had to be considered coincidently in the field and cannot be entirely separated in reporting upon field work.

In the following sub-sections they are discussed as they were studied, interdependently.

III (*a*). **Experiment to test the Movements of Flies along the Lake Shore.**

The larger catches of fly made on Bulago Island and recorded in Table I were from near the extremity of a long, narrow spit of sandy land designated in the notes as "Crocodile Point" (see Fig. I). The area of this spit was considerably less than of the islet of Lula, from which the flies were caught as recorded in Tables VI and VII. But though these catching experiments on Lula quickly brought about reduction in density of active flies, it was observed that no such effect was produced on the density of the fly at Crocodile Point. On the contrary, although more than 2,000 flies were caught there during the period 10th to 13th November, neither density nor female percentage underwent notable change (see Table XII).

TABLE XII.

Catch of Fly at Crocodile Point, Bulago Island, showing Existence of Rapid Movement along Shore.

Date.	Catch of Fly.		Density of Active Fly.*		
	Total.	Females.	Males.	Females.	Total.
5th November 1913	564	27 %	14·2	5·8	20·0
10th " "	630	20 %	16·0	4·0	20·0
11th " "	944	28 %	12·5	5·0	17·5
12th " "	167	18 %	10·3	2·4	12·5†
13th " "	435	29 %	14·7	6·0	20·7
Totals and averages 1st experiment	2740	24·4 %	13·5	4·6	18·1
17th January 1914	912	40·3 %	24·4	17·1	42·5
20th " "	1102	48·2 %	27·5	26·4	53·9
21st " "	303	44·2 %	11·3	9·0	20·3†
22nd " "	606	48·0 %	26·5	28·9	55·4
Totals and averages 2nd experiment	2923	45·2 %	22·7	20·3	42·9

* "Density" is the number of flies caught per fly-boy per hour.

† These days were somewhat dull and overcast, rendering flies inactive.

The fact that density of both sexes was perfectly maintained on the 13th November after four consecutive days of catching, when viewed in the light of the results of less extensive catchings on Tavu (Table V) and Lula (Tables VI and VII), can only be explained by the movements of fly along shore, and these movements must be quite free and rapid in order to account for it.

Notwithstanding the semi-isolated position of Crocodile Point, as many flies penetrated its area each day as were caught on it, leaving no other conclusion possible than that, if no flies had been caught, as many would have moved away from it. Otherwise stated, the fly population of this region was so far from permanently fixed there that hardly any individuals sojourned there for more than a single day.

The experiment of the 5th to 13th November 1913 was repeated on the 17th to 22nd January 1914 (Table XII) and completely confirmed it. The conclusions were subsequently confirmed in various other ways, and there is no doubt that the flies of this species move freely about from place to place, forming continuous streams of fly traffic along the shores of lakes, banks of streams, and, it was subsequently ascertained, along the borders of woodland, game trails or human pathways, etc.

III (*b*). **Movement of the Sexes along the Lake Shore.**

Although it was impossible to reduce the local density of fly under such conditions as exist at Crocodile Point if an interval of several hours is permitted to elapse between periods of catching, it was easily possible to reduce the density of male flies—not of active females—by even a single hour's catching, provided no interval elapsed before the experiment was repeated. In other words, if catching is continued over several consecutive hours, the density of male flies, but not of active females, will be reduced during the first hour, and will not rise again to normal until several hours have elapsed.

TABLE XIII.

Catches of Fly for consecutive hours at points on Lake Shore, showing Reduction in Density of Males but not of Active Females, and demonstrating more rapid movement of Females.

Locality.	Date.	Hour.	Catch of Fly.		Density of Active Fly.		
			Total.	Females.	Males.	Females.	**Total.**
Crocodile Point, Bulago Island	17th Jan. 1914 ..	1st	343	30·9 %	35·0	14·1	**49·1**
		2nd	319	41·4 %	26·7	18·5	**45·2**
		3rd	250	56·2 %	14·5	18·7	**33·2**
Landing Place, Tavu Island .	15th Jan. 1914 ..	1st	419	10·7 %	62·3	7·5	**69·8**
		2nd	250	10·4 %	37·4	4·3	**41·7**
		3rd	183	21·3 %	24·0	6·5	**30·5**
		4th	163	25·2 %	20·3	6·8	**27·1**
		5th	167	26·8 %	20·3	7·5	**27·8**

These experiments were many times repeated with results similar to those presented in Table XIII. It was found that the local density of male flies could be very quickly and easily reduced, whereas that of active females was not affected in this manner. It was conclusively proved by experiments cited on p. 365, and illustrated by Table XII, that reduction in density of males would be made good by incoming flies if some hours were allowed to elapse before a second catch was made, but that no period of waiting was required to make good any reduction in density of active females caused by catching.

The only conclusion that can be drawn is that the active females habitually move along shore much more rapidly than the males, or than many of the males. This is entirely in accord with the conclusions reached through experiments cited in Sect. I, that active females are hungry, and actively seeking food, and that degree of activity is correlated with abundance or scarcity of food. Their movements along shore are stimulated by hunger. The movements of the males are in part stimulated by hunger, but also in part (see Sect. IV) by sex instinct. The object of the females—and of such males as require it—is to seek food; the object of many of the males (forming a majority when females are inactive and the female percentage low) is merely to seek the females, and this is accomplished by loitering along the routes most freely followed by the food-hunting flies.

This conclusion found ample confirmation as the investigations progressed; as, for example, by the fact that when food is so scanty on an island (as on Kimmi Island in January 1914) that the female percentage is very high, it is impossible to reduce the local density of either males or females by catching experiments at points where they are passing. Under such conditions nearly all flies are seeking food, and all are equally active, as clearly shown by a comparison between the figures presented in Table XIV and those presented in Table XIII.

TABLE XIV.

Catch of Fly at a point on Shore of an Island where Food was deficient, and where nearly all Flies were seeking it, showing equal degree of Activity on the part of both Sexes.

Locality.	Date.	Hour.	Catch of Fly.		Density of Fly.		
			Total.	Females.	Males.	Females.	Total.
Landing Place, Kimmi Island	26th Jan. 1914 ..	1st	205	66·3 %	23·0	45 2	68·2
		2nd	249	66·3 %	28 0	55·0	83·0
		3rd	451	65·2 %	26 1	49·0	75·1
		4th	463	69·9 %	27·0	50·0	77·0
		5th	289	64·0 %	17·3	30·8	48·1*

* Falling off in density during the 5th hour was due to approach of evening. The sexes remained proportionately as active as before, as shown by the female percentage for this period.

III (*c*). Effect of Shelter, or of Type of Vegetation, upon Long-shore Movements of Fly and upon Percentage of Females in the Catch.

On 4th September 1914, a catch of fly was made under unusual circumstances on the island of Bukassa. The shore at this point was lined with a very dense fringe of reeds only two or three yards in width. Inside the fringe was open grass land, cropped very short by hippo, with scattered clumps of thick bush and trees of a sort affording attractive shelter to fly. At the observation point itself was a landing place of hippo with a trail forming a tunnel through the reeds. The prow of the canoe was thrust into this tunnel, with the stern projecting beyond the reeds into the open lake, and collections were made simultaneously by one boy stationed in the stern of the canoe, *outside* the thick fringe of reeds, and by two boys at and near the point where the hippo trail entered the opening, *inside* the fringe of reeds. These reeds, it should be noted, were at least 10 feet in height, or higher than tsetse is at all likely to rise from the ground.

The three boys worked for two hours with the following results:

	Inside Reeds.	Outside Reeds.
Catch per boy hour—		
Males	3·0	3·5
Females	·5	7·5
Female Percentage	14·3%	68·2%

The extraordinary feature of this catch was the low percentage of females (14·3) *inside* and the high percentage (68·2) *outside* the barrier formed by the reeds; the two points being separated by not more than 10 yards.

This same phenomenon was observed a second time under different conditions in a catch made on the 23rd September 1914 at a point on the island of Bussi, where two boys worked ankle-deep in water outside a thick mass of reedy vegetation that prohibited landing, and two other boys on a point of shelving rock, backed by an open space and bushy forest of a type much favoured by fly as shelter. The poorly sheltered, reed-fringed point on the shore was only about 100 yards distant from the attractively sheltered point.

The catch was as follows, for the four boys for half an hour:

	Well sheltered Point.	Poorly sheltered Point.
Catch per boy hour—		
Males	49·0	8·0
Females	3·0	13·0
Female percentage	5·8	60·8

As before, there is an extraordinary discrepancy in sex ratio between points separated, in this case, by only about 100 yards. And in both cases the high percentage of females is associated with a type of vegetation known to be especially repugnant as shelter and the low percentage with a type of vegetation known to be attractive.

A hypothetical explanation for this phenomenon, which has withstood all tests applied to it, is as follows:—

(*a*) The body or mass of active flies is continually in movement, and streams of flies are continually passing points along shore (see Sect. III (*a*)).

(*b*) These streams of moving flies are made up of (1) food-hunting flies of both sexes, which compose a variable proportion dependent upon abundance of food and which move rapidly; and (2) male flies which are not seeking food, but which frequent the routes followed by food-hunting flies, and which move much more slowly (see Sect. III (*b*)).

(*c*) The relatively idle and lingering males tend to prolong their sojourns at points where sheltering vegetation is of the most attractive type, and to pass quickly, or not at all, by points where the vegetation is of an unattractive type. It follows that (1) density of active males will be greatest where shelter is most attractive, and least where it is least attractive, and (2) that the percentage of females amongst caught flies will be greatest where shelter is least, and least where shelter is most attractive to the lingering males (because food-hunting flies must, for several reasons,* consist principally of females).

When confirmation of this hypothesis was sought it was found on every hand, not only in new catching experiments and fly survey work, but in old records, made

* These reasons include the following:—

1st. Because the females in any district or region appear to outnumber the males (see Sect. I (*d*)).

2nd. Because the females must nourish their young as well as themselves, and most probably require food somewhat more frequently, in nature, than males.

3rd. Because the males are normally active at all times during good weather, and are more apt than the females to encounter host animals without specifically seeking for them.

ong before. The records made on the island of Kimmi in January 1914 are an example. As presented in tabular form (Table XV) they are not particularly

TABLE XV.

Catch of Fly on Island of Kimmi showing effect of variable character of Shelter on Density, Sex Ratio and Movements of Glossina palpalis.

Date. (January 1914.)	Locality on Island. (Observation Point.)	Catch of Fly.		
		Male Density.	Female Ratio.	Total in Catch.
27th ..	South-easternmost point	39·5	53·2	506
29th ..	North-eastern point	15·7*	66·9	142
29th ..	North-western point	43·3	52·2	272
24th ..	South-western point	23·3*	62 9	384
27th ..	Southern shore	42·7	53·0	276

* Shelter was appreciably less attractive at these two points.

striking, but the correlation between shelter, local density of males, and female percentage is quite strikingly shown in figure 2. In this case the " shore line " in the graph represents the entire circumference of the island, a distance of between 2 and 3 miles, with five observation points located as stated. The difference in character of shelter was not particularly notable, but it was enough to produce the effect shown.

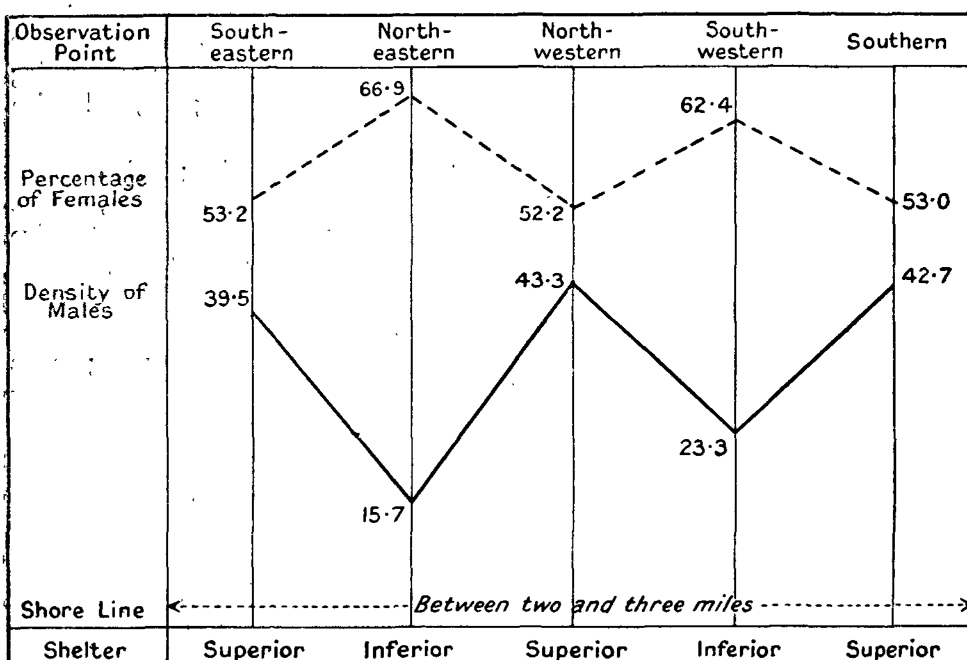

Fig. 2. Graphic representation of data given in Table XV.

Records made in the course of the fly survey of Bugaba Island as presented in fig. 3 afford a second excellent example of the correlation between character of sheltering vegetation, density of male flies and percentage of females in the catch. In this particular case there was a short reach of sandy shore at observation point 43 which served as a breeding ground for the flies, but which was poorly (too slightly) sheltered. At either end of this bit of sandy shore was forest, with marshy, reed-grown fore-shore of a distinctly unattractive type. Only where the forest growth came down to the more open sandy shore at points 42 and 44 was shelter really attractive

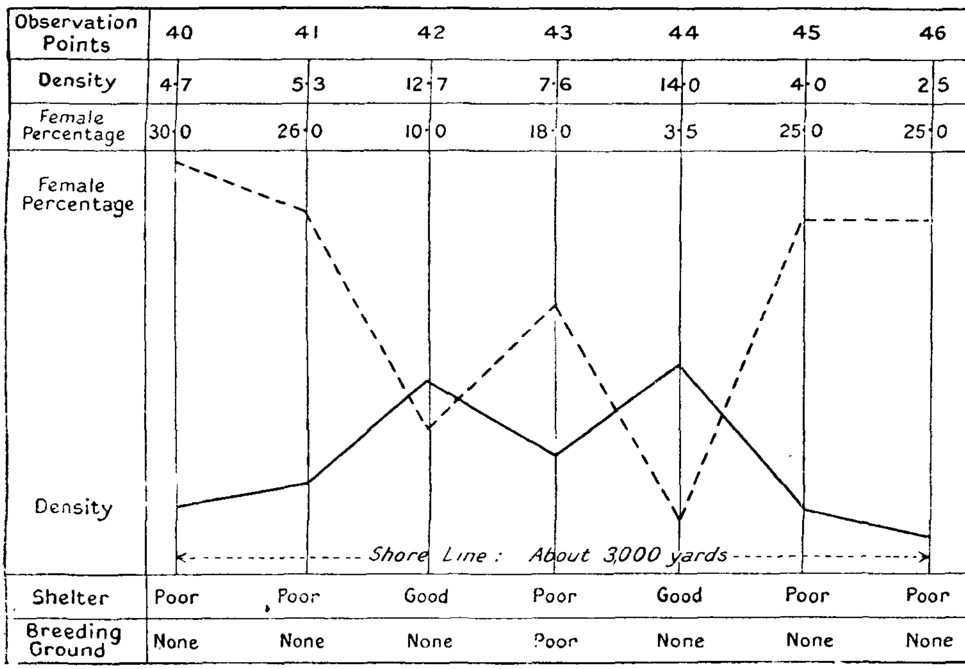

Fig. 3. Correlation between character of shelter, density of male flies and percentage of females.

Figure 3 shows an excerpt from the data secured during the " fly survey " of the island of Bugaba (vide Sect. VI. (*g*)) and illustrates conditions of infestation by fly along a reach of shore about 1⅝ miles in length. In all, more than 150 miles of mainland and island shore were systematically surveyed in this manner, and the data secured have served in scores of cases to confirm the conclusions herein stated concerning the correlation between character of shelter, density of males and female percentage.

A single other example may be given in Sect. III (*d*) which follows.

III (*d*). **Notes on Survey of Lutoboka Bay, Bugalla (Sesse) Island.**

Figure 4 presents the results of a survey of some 5 miles of shore, principally included in the large circular bay that lies within the peninsula of Lutoboka on Bugalla (Sesse) Island. This survey was undertaken with the object of collecting data relative to the effect of environment upon range and density of *Glossina palpalis*.

It is impracticable to include in the graph data concerning environmental features responsible for the striking variations in male density and sex ratio shown by the curves. In general they are as follows :

Points 1 to 4 inclusive are typical of shore infested to slightly above the average extent for this general region. This reach of $1\frac{1}{2}$ miles lies on the western shore of the bay, and is densely wooded, with bits of open shore alternating with reed-grown and jungly reaches. There were some sand and gravel deposits affording good breeding grounds.

Points 5 to 8 inclusive :—The forest continues, but there is no more open shore, nor any breeding places. Instead there is a fringe of floating sudd (papyrus and saw-grass) lying off-shore and no open space between it and the massive shelter of the forest behind. Catches were made from a canoe outside the sudd, which, with the exception of grass, is the most repulsive type of vegetation.

Only the hungry food-hunting flies (principally females) pass beyond the limits of the open shore at point 4. The relatively idle males turn back.

The minimum density of males and maximum percentage of females is recorded from point 6. At point 7 males are more numerous and female percentage has fallen, indicating that a new fly colony is being approached. The catch at point 8 confirms this and makes it certain that males are coming into the repulsively sheltered reach from the other direction.

At point 9 there is a break in the sudd, and an open grassy bit of fore-shore, scattered with bushes and backed by massive forest. Shelter is attractive, but as yet no breeding grounds occur. The excellent shelter makes for a sharp increase in male density and a corresponding decrease in female percentage.

At point 10, the forest, which has continued unbroken until now, ceases and open grassland comes down to near the water's edge. The foreshore is open, with scattered bushes, and deposits of beach sand afford excellent breeding grounds. For a short space between points 9 and 10 this series of open sandy belts is backed by the massive shelter of the forest. This combination affords complete protection to the flies, both as pupae and adults, and forms the centre of the colony, or centre of infestation for the shore on either side.

Beyond point 10 the open fore-shore, with sand deposits and the slight shelter of scattered bush, continues (as at point 10), but is no longer backed by massive shelter. The effect on male density and female percentage is precisely as caused by the fringe of sudd. The idle males turn back when massive shelter ends, and only the food-hunting flies, in part, continue.

At point 14 is a relatively thick mass of bush, which tempts a few males to linger, but not for long, and density does not rise again until, some distance further on, forest shelter is again encountered.

There is not the slightest doubt that in these observation points high percentage of females coupled with low density of males is due to insufficient or unattractive sheltering vegetation, leading to a partial segregation of the food-hunting flies of both sexes from the relatively idle and satiated males

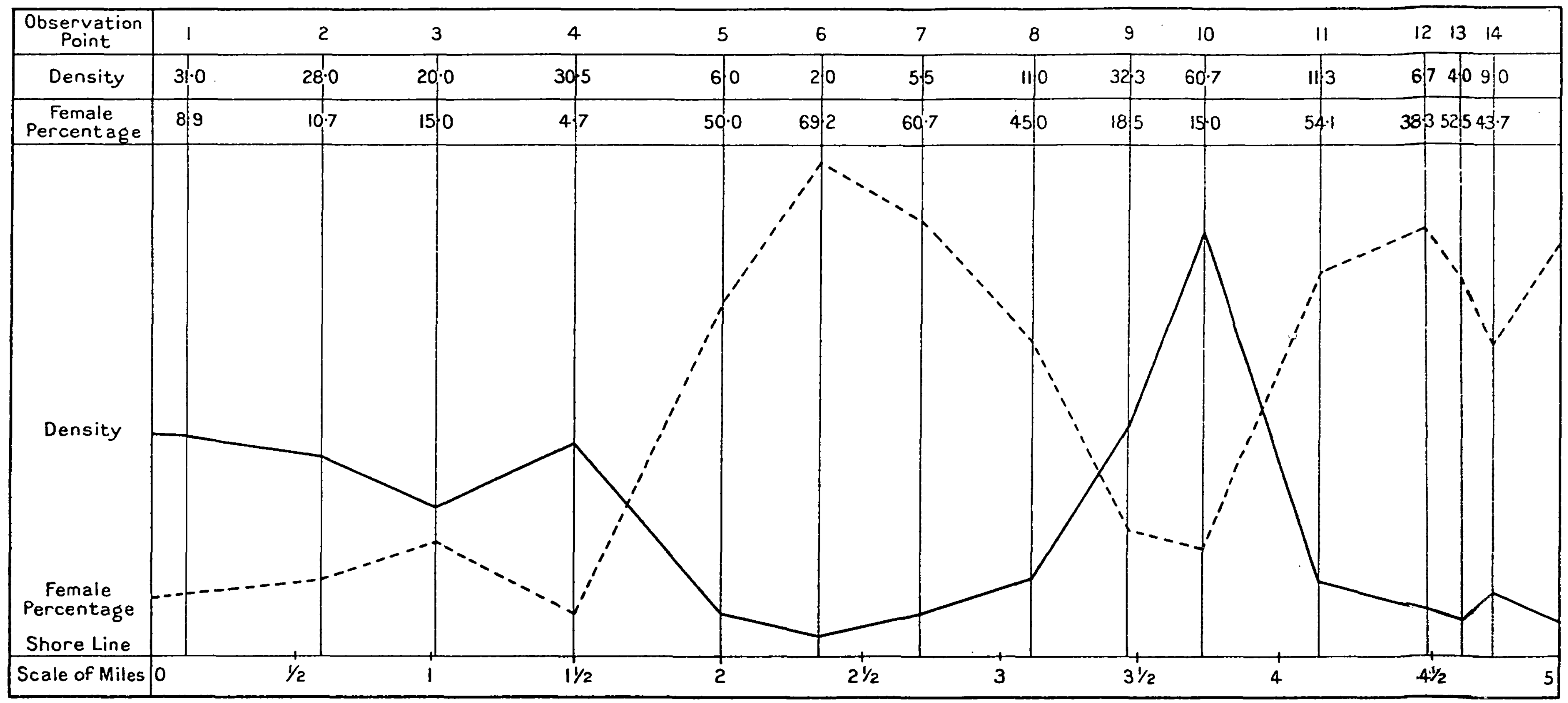

Fig. 4. Fly survey of a reach of shore in the district of Lutoboka, Island of Sesse (Bugalla), illustrating effect of environment on range, density and movements of Glossina palpalis.

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III (*e*). Maximum Percentage of Females brought about by Segregation through Movements.

The maximum percentage of females amongst active flies encountered at any point on island or mainland was in the district of Buddu between the old landing places known as Kalkosa (or Sekwe) and Bale. The figures of the catches made during a fly survey of this coast are presented in Table XVI. The distance from

TABLE XVI.

Catch of Fly in the Mujuzi Colony.

Date. (June 1915.)	Observation Point.	Catch of Fly. Males.	Females.	Total.	Density of Males	Percentage of Females.
24th	40	26	39	65	26·0	60·0 %
24th	41	12	90	102	4·0	88·3 %
22nd	42	33	65	98	16·5	66·0 %
22nd	43	23	68	91	11·5	76·2 %
22nd	44	58	157	215	19·3	73·0 %
24th	45	196	162	358	98·0	45·3 %
22nd	46	106	103	209	53·0	49·2 %
26th	47	41	73	114	20·5	64·0 %
26th	48	45	120	165	19·3	72·7 %
26th	49	20	84	104	10·0	80·8 %
26th	50	10	80	90	5·0	88·8 %
Totals and averages ..		570	1041	1611	26·0	67·6 %
Average by points ..		..	..	..	26·6	69·5 %

point 40 to point 50 is about $3\frac{1}{3}$ miles. Point 45 is at the mouth of Mujuzi Creek, which affords excellent harbour for crocodiles, as well as breeding places for the fly on its banks. It is the colony centre, and centre of infestation for a considerable reach of shore. Points 47 to 50 are in the Bale fly beach mentioned in Sect. II (*a*), Table VIII.

The average female percentage for this district is either 64·6 or 69·5 according to the method of computation, and compared with the maximum encountered on the islands (57·5 or 64·6 for the colony on Kimmi Island; vide pp. 363 and 370) is about 6·0 points higher. This is undoubtedly due to scarcity of food, which only occurred sufficiently or at all at the very mouth of Mujuzi Creek (point 45). The behaviour of flies bore this out completely. Nowhere else on island or mainland were they so troublesome; it was impossible to avoid being bitten, even with both hands employed wielding fly switches.

The extraordinarily high proportion of females at points 41, 49 and 50 break all records made elsewhere (for equally large catches), and are certainly explained by the unattractive character of the environment* at these points retarding the movement of the relatively idle and inactive males along shore. These males were concentrated along the short reach of shore including points 45 and 46 ; and elsewhere it was almost entirely the actively moving, food-hunting flies that were caught.

This particular colony of Mujuzi is in several other respects one of the most interesting and deserving of study of any encountered on either island or mainland. It is mentioned elsewhere, and a graph of it is presented facing p. 388. It was non-existent in 1906 but came into being subsequently as a result of environmental changes described on p. 458.

III (*f*). The Full Significance of the Phenomenon of Sex Disparity in *Glossina palpalis* with Relation to Food Supply, Shelter and Movements of Fly.

The phenomenon of a variable ratio between the sexes of active flies of *Glossina palpalis* proved on investigation, as I have attempted to make clear, to be replete with interest and significance.

Taken over any considerable district or region it is a fair index to the abundance of preferred hosts, and thereby of the relative immunity of man to attack (see Sects. I and II).

Taken locally, point by point along a reach of shore, and coupled with the local density of active males at these same points, it becomes a subtle index to the attractiveness or repulsiveness of the local environment to fly. This fact having been conclusively proved, thereafter data in such local variations become of really great value in reaching conclusions concerning the relative attraction of various types of vegetation, etc., to the flies.

Finally, through study of this sex disparity and its causes, a very clear conception is obtained of the ordinary movements of the flies along the shores of the lake, banks of stream, borders of woodland, game trails, foot-paths, or other favourite courses. A great many little experiments and informal observations were made to ascertain the routes most freely followed by the active food-hunting flies—too many to mention in detail. The lake shore is the most favoured of them all, but, in general, they follow quite closely the line separating sunlight from shadow.

The flies are averse to penetrating shadow, unless sunlight is perceptible beyond, and even more averse to crossing sunlit spaces unless shadow or massive shelter is perceptible beyond.

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* It was not necessarily unattractive shelter that prevented the males from congregating at these particular points. They were distant from all sources of food, and however attractive shelter may have been (it was in fact very attractive at 49 and 50, but not at 41) no permanent concentration of males could occur.

The males tended to congregate at point 46, which was well sheltered ; but not at point 44, just the other side of the creek, where shelter was not attractive. But by the time the relatively idle males had dispersed much beyond point 46, towards points 49 and 50, they began to require food, and there was no food unless they passed back to point 45, or passed far beyond point 50.

In other words, a reach of foodless shore, although supplied with both shelter and breeding ground, produces the same falling off in male density and elevation of female percentage as the shelterless shore described in the pages preceding this.

It was found by experiment, details of which need not be given, that flies will cross open channels up to at least 300 yards in width, but that they do not cross them very freely. It is certain that the width of the channel likely to be crossed is dependent on the character of the farther shore. Certainly they do not cross much wider channels than 300 to 500 yards at all freely, for from the beginning evidence of their doing so was carefully sought, and no shred of it secured.

It is the movements of fly along shore, or along the border line between sunlight and shadow, with which we are principally concerned, and these studies have shown how the flies tend to congregate in attractively sheltered localities, where, in consequence, density of males is high and percentage of females low, and how, pressed by hunger, both sexes, but more especially the females, tend to disperse from these centres of greater density and range along the lake shore or other favoured route in search of the sluggish amphibian animals on which they principally feed, thus accounting for the extraordinary preponderance of females amongst caught flies in repulsively sheltered localities.

IV. The Assembling Habits of Glossina palpalis.

The stimuli which keep in motion the streams of tsetse described in the preceding section are known to include, and believed in all ordinary circumstances to be limited, to the following:—

(A) *Hunger.* Every second or third day the flies of both sexes undertake food-hunting flights. These are relatively rapid and easy to follow.

(B) *Self-protection.* At the close of each period of activity the flies of both sexes are moved to seek massive shelter, where they remain in seclusion during periods of inactivity. They appear very unwilling to move far away from such shelter; hence flights in search of it are usually of short duration.

(C) *Maternal Instinct.* At intervals of eight days, or longer, the females are stimulated to seek breeding grounds wherein to deposit their young. The great concentration of puparia in very attractive breeding places is proof that flights in search of them were of considerable duration. The location of deposits of puparia near the well-marked courses followed by food-hunting flies is proof that these are followed. But the flights themselves are very hard to follow.

(D) *Masculine Instinct.* Every day, if the weather is good, the males appear all to leave shelter to undertake assembling flights. These are readily followed, and as described in the preceding section, are relatively slow. The insects tend to congregate or to loiter at points or along courses where the females are most likely to congregate or to pass. It is these special activities which are now to be considered.

Several points in connection with the assembling habits of *Glossina palpalis* in addition to those touched upon in the preceding sections are discussed in the sub-sections following. The topic is inter-dependent with several others, including, especially, host preferences of the flies.

IV (*a*). **The "Following Swarm" of** *Glossina palpalis.*

Many observations, but few detailed experiments were made upon the curious habit of *Glossina palpalis* of approaching and scrutinising strange objects. It was noted that there is ordinarily little discernible difference in this behaviour toward inanimate and animate objects other than their favoured hosts. When the percentage of females amongst active flies is low, man is almost immune to attack, but his person is none the less, and equally with any other similarly conspicuous object, strangely attractive both to the food-hunting flies of both sexes, and to the relatively inactive males. It is on this account that the males are so easily caught, whether or not they are seeking food.

Of all objects, apart from their favoured hosts, the most curiously attractive to flies is, perhaps, an open dark-coloured umbrella, and in the catching experiments and fly survey work the fly boys were each provided with one. When displayed at any point in or near the course followed by food-hunting flies, or the relatively inactive males, it becomes so conspicuous an object as to attract to it virtually all flies which perceive it. They crawl over it, especially its underside, inspecting it curiously until curiosity is satiated—or for, perhaps, one to five minutes—when they pass on. And this is equally true of both idle males and food-hunting individuals of both sexes. Despite the extraordinary attraction of the object there is no tendency on the part of any flies to linger more than the few minutes required for its inspection, so that a swarm will never collect. If the density of the stream of passing flies is 20 or 30 per hour, there will be from one to four or five flies resting on the attractive object at all times, but the same flies do not remain for long.

As above stated, the behaviour of the flies toward man is, ordinarily—*i.e.*, when the man is alert, food is plentiful and the female percentage low—indistinguishable from their behaviour toward his coat thrown over a bush or his umbrella openly displayed. It is not necessary to think about the flies or to ward them off; occasionally one will bite, but the number doing so is so small that it is not worth thinking about. Man is attractive to flies, but does not hold them after their curiosity is satisfied. The same is true of goats, sheep, and many other animals.

But with certain animals under certain conditions the behaviour of the flies is conspicuously different. When a crocodile or *Varanus* is basking in half open sunlight, the flies attracted to them are apt not to pass on, after cursory examination, but to linger indefinitely. The result is the gradual accumulation of an accompanying or "following" swarm, which may grow to number several times more flies than a boy stationed at the same spot would be able to catch in an hour's time, and which may certainly represent (sometimes) the accumulation of the majority of flies passing the spot during several hours' time. Similar swarms may collect upon or near a foraging *Varanus*, as it wanders slowly through the woodland, or a grazing situtunga, and may then follow the animal out of woodland into open grassy spaces, where the flies would not go of themselves.

Mention of these conspicuous swarms of flies in connection with *Varanus*, crocodile, tortoise, hippopotamus and situtunga is made in Sect. VI (*e*). A few additional notes excerpted from my field books follow.

On Varanus. Kitobo Island, 3rd December 1913.

Varanus observed excavating burrow in sandy soil some little distance from shelter. On approaching it made off rapidly, and on reaching the spot I was assailed by a great number of tsetse, which swept back and forth and around me like angry bees, " buzzing " in their flight in a manner never before noted. After a few minutes they all dispersed, without any of them alighting upon me.

On Varanus. Nsadzi Island, 3rd February 1914.

A *Varanus* was suddenly flushed in grass land (grass about knee-high) not much less than a hundred yards from any shelter. It made off rapidly and a swarm of flies, numbering several dozen at least, rose and filled the air with their angry, bee-like " buzzing." As on Kitobo they swept back and forth and around about me, but none alighted or offered to attack, and in a minute or two all had dispersed.

On Situtunga. Bugalla Island, 23rd November 1914.

A large male situtunga was approached as it was feeding with its head concealed in a dense thicket. With glasses (Zeiss prismatic $\times 12$) it was possible to make out that a peculiar dark colour of fore leg, lower shoulder and thorax, which were plainly seen through an opening in the bushes, was due to an unprecedented number of tsetse, which literally blackened its coat. It seemed entirely unmoved and phlegmatic under attack.

On being shot, the animal plunged directly through the thicket; ran a few yards at great speed and fell. On proceeding to the spot where it was feeding, I found a " following swarm " of fly of unprecedented size (probably not less than 200 flies) buzzing like a great swarm of angry bees. They surrounded me, but hardly any alighted on me or followed me to where the antelope lay.

On Situtunga. Damba Island, 13th September 1915.

A large male situtunga was shot in an opening in the forest in the dusk of evening. It ran into the thickly shaded forest and fell. On reaching it I was amazed to find a considerable swarm of flies, partly outside, but judging by the noise they made, more inside than outside the forest (it was so dark inside they could not be seen). Is it possible that a swarm will follow an animal into the night, and perhaps remain on its body all night?

On Varanus. Manene Island, 16th March 1915.

While passing through forest a movement in the vegetation (the ground was completely covered with broad-leaved herbage rather less than knee-high) indicated the approach of some small animal. It proved to be a *Varanus*, which came very slowly, evidently hunting insects and molluscs, to very near me. At no time could I see its body, but keeping pace with it and evidently following the movements of the herbage was a swarm of perhaps two dozen tsetse. The flies were not anxious to feed or to reach the body of the animal, but merely followed its movements, alighting on the herbage or hovering about. A movement on my part sent the animal scuttling rapidly away, whereupon the disappointed flies rose and swept back and forth, buzzing angrily as usual in such cases.

On Situtunga. Bugalla Island, December 1914.

(Original note lost.) On entering an open space in the jungle where formerly were plantations, a small herd of two female and two half-grown male situtunga was seen, with other animals feeding in the edge of the jungle out of sight. Those in sight did not immediately see me, who stood motionless watching them, nor upon seeing me did they betray alarm or more than mild curiosity. The whole herd moved in my direction and one female approached within three yards. Each animal was followed by a small swarm of tsetse—perhaps 15 or 20 flies—few of them on the animal itself, but principally on the vegetation close at hand, or hovering about. Not one of the flies was seen to feed, nor did the animals show annoyance at their presence. On becoming alarmed the antelopes made off without undue haste, the flies following.

The above may serve in some manner to make clear the difference between the behaviour of fly toward a favoured and complacent host, and such another as man, who is neither favoured nor complacent. Anyone passing through infested territory and aware of two or three, or perhaps half a dozen, tsetse constantly hovering about him is certain to receive the impression that this number of flies is persistently following him. In the case of *Glossina morsitans* the impression would, probably, be correct, for man will collect a following swarm of this species; but with *Glossina palpalis* it is incorrect. The same individual flies will not follow a man for more than a few minutes unless they are very hungry, but will quickly drop behind and be replaced, perhaps by others. This is easily proved by catching them just as they appear; one will quickly catch many times more than appear to be following at any one time.

The explanation of the "following swarm" with *Glossina palpalis* is, without doubt, identical with that put forward by Lloyd for the "following swarm" of *Glossina morsitans.* It is the assembling habit of the males; first, to linger along the routes followed by the food-hunting females; secondly, to examine any strange object coming in range of vision; and finally, on encountering a complacent host of a favoured species, to remain by it; for in these ways they are most likely to come into contact with the seclusive females.

Nothing else in the habits of the fly affords more convincing evidence of their unwillingness to feed upon man, unless they are forced by hunger. Far from attracting a following swarm, man cannot even hold one that has already been attracted to some other host; if by his approach he startles the favoured host into flight, there is not the slightest tendency on the part of the following flies to turn their attention to him, but invariably, as in the cases noted above, the swarm has dispersed without the flies paying as much attention to the intruder as is usual when other hosts are about.

IV (*b*). **Conditions under which a Following Swarm will Collect.**

More than 25 separate experiments were made with various wild and domestic animals tethered at points where they were exposed to columns of food-hunting flies, mainly to ascertain the host preferences and feeding habits of the insect, and finally in a specific effort to induce a "following swarm" to collect under observation. In the very first experiment in the series such a swarm did collect upon a tethered *Varanus*, but all other experiments failed in this respect.

Under entirely natural conditions swarms had been seen on *Varanus*, situtunga, crocodile, hippopotamus, pig (of domestic stock, but run wild) and tortoise, and most freely of all on *Varanus*. The fact that repeated attempts to induce one to form on *Varanus* which were held in constraint all failed, excepting only the first (see Sect. VI (*c*), experiment 4), convinced one that something more than the mere presence of a host animal of a favoured species is necessary, and failure is believed to be due to the impatience of these animals under restraint. In other words, a host must be complacent under attack as well as of a favoured species or it will not be favoured by tsetse to the extent of attracting a "following swarm."

The final experiments with *Varanus*, sheep and oxen are described in Sect. VI (*c*), experiment 3. They led to the conclusion that a host to be "favoured," must always be complacent, and suggested that perhaps almost any of the larger animals, including man, might be favoured, even to the extent of collecting a "following swarm," if it were in them to suffer the attacks of *Glossina* without sign of protest.

V. The Effect of Open Water and Humid Conditions upon the Range of Glossina palpalis.

No factor in the bionomics of *Glossina palpalis* is more obviously correlated with the range or distribution of this species than open water. It is a riparian species, and its occurrence far from shores of lakes or banks of streams is a subject for remark whenever observed.

Exceptional dispersion inland, however, is not at all rare, and many cases of it were encountered and studied. In all cases the explanation was the same, and involved, as virtually every topic in *Glossina* bionomics seems bound to involve, the subject of hosts and host preferences. The two topics are inseparable in field work and cannot well be separated in discussing and recounting field work.

These studies were more convincing to the observer than it is feared they may prove to the reader, that the correlation in question is purely coincidental; that water or humid conditions are not of direct benefit to the insect, nor required by it; but that a proper combination of food, shelter and breeding places which is requisite to its existence occurs so infrequently away from the shores of lakes or banks of larger streams that it is perforce riparian in habit.

V (*a*). **Range of Fly inland from Lake Shore.**

Ordinarily the range of fly inland from the lake shore is extremely limited; at 50 yards there will usually be a sharp reduction in density; beyond 100 to 200 yards flies will appear only as stragglers; and at 300 to 500 yards they will disappear, or, at least, density will drop below any figure that can be conveniently measured. If range inland is more extensive than this, some special cause for it must exist.

Attempts to measure the ordinary inland range of fly were limited to a single experiment on the island of Kitobo in December 1913, which resulted as follows—the catch being made at the base of a slope that rose rather steeply to a plateau with abandoned plantations.

Catch at base of slope, 5¼ "boy hours," showed density (both sexes) of	15·50
Catch half-way up slope, 16 "boy hours," showed density of	1·05
Catch at crest of slope, 28 "boy hours," showed density of (This point was well under 300 yards from the water's edge.)	·26
Catch in old plantations beyond the crest of slope, 14 "boy hours," was	Nil.

This is probably a sharper decline in density than usual, but not excessively so

V (*b*). **Effect of Marshes and Rivulets on Range of the Fly.**

The effect of lakes or streams on the range of *Glossina pa palis* is so conspicuous that whenever any unusual extension of its range inland from lake shore or bank of large stream has been observed it has almost always been accounted for as being due to presence of small streams, marshes or humid conditions of life generally. Therefore if any island were to show inland range of fly too much in excess of that noted as "normal" in the preceding sub-section, the question of interior conditions with respect to water and elevation (dryness) is the first to be considered.

A survey of the islands was begun in January 1914 to ascertain and measure variations in degree of local infestations, as they might be correlated with differences in local environment. Mostly small islands, of less than 1,000 yards short diameter, were visited; but by the 1st September out of a total of some 40, 8 of larger size had been included in the survey, and conditions with respect to infestation by fly, humidity and topography of the interior of each of these islands were found to be as stated in the accompanying table (XVII).

TABLE XVII.

Fly Survey of Islands in Victoria Nyanza showing Lack of Correlation between Humidity of Interior and Infestation by Glossina palpalis.

Island.	Conditions in Interior		Infestation by *Glossina.*	
	Topography.	Humidity.	Shore Line.	Interior.
Wema	Hilly	Dry†	Dense	None.
Damba	Flat	Streams and marshes ..	Dense	Medium.
Kome	Hilly	Streams.. ..	Light	None.
Kitobo	Plateau	Dry*	Medium.. ..	None.
Bukassa . ..	Hilly	Dry*	Light	Light
Bugaba :. ..	Hilly	Streams.. ..	Light	None.
Bubembe ..	Hilly	Dry†	Light	None.
Bugovu . ..	Hilly	Dry†	Light	None.

* Careful survey showed no streams near points of interior infestation.

† Streams may exist on parts of islands that were not explored.

It will be seen that of the eight islands listed, two differed from the rest in being infested in the interior. One of these, Damba, is flat, with streams and marshes in its interior, and with a dense infestation of fly along shore. Two others—Bugaba and Kome—also had streams flowing down from the hills, but they were hilly and the infestation along shore was light. Either elevation or lightness of infestation along shore might be a possible explanation for absence of fly inland, and its absence is merely negative evidence that it does not always occur in humid localities near lake shore colonies.

But in the case of Bukassa Island we have a dry, hilly interior, with only a light infestation along shore, and for all this a general infestation of the interior. This is not negative, but is absolutely positive and very strong evidence that, whatever it may be which restricts the range of this tsetse to a narrow belt along the shore of the islands generally, it is *not* the presence of water or soil humidity, for the interior of Bukassa is, perhaps, the driest and hilliest of any of those listed except Wema. And whereas it is perfectly possible that the presence of open water might account for infestation by tsetse of a belt several miles in width along the borders of it, it is impossible to consider water alone as the determining factor when, on some islands, the inland range of fly is virtually limited to 500 yards or less, whereas on others it is extended to 1,500 yards and more, and with no surface water in sight.

Slight though this evidence is, it is of such a positive character that it is practically conclusive. Some other factor than open water must be held accountable for limitation to inland range of *Glossina palpalis* from shores of lakes or banks of streams.

V (*c*). Effect of Food Supply on Range of the Fly.

A comparison between the two islands, Bukassa and Damba, in search of points of similarity, which should at the same time be points of difference between these and the other islands named in Table XVII, led to the conclusion that the most probable explanation for their infestation interiorly by tsetse was the presence of unusually large numbers of game animals : of situtunga on Damba, and of domestic pigs run wild on Bukassa. This conclusion was reached reluctantly, because at that time (September 1918) it was believed that the only favoured hosts of this species of tsetse were reptilian.

The course of the fly survey of the islands was thereupon set to include careful study of conditions on all such as were known or suspected to be more than usually well stocked with game. These included specifically the group of semi detached islands of Bukone, Serina and Lulamba, and the island of Buvu, upon which pigs were known to occur, and the (relatively) very large island of Sesse (Bugalla-Buninga), which had been reported to be overrun with situtunga.

Examination of the pig islands disclosed the fact that though great numbers of the animals had been present (enough to cover them with networks of trails and to uproot the soil nearly everywhere in the woodland) some great catastrophe had reduced their numbers to a few stragglers. More skeletons were found than traces of living animals. But one result of the visit was to discover a "following swarm" of fly about a pig that was shot, and to prove conclusively enough that this animal may be a favoured host. None of the islands was found to be infested by fly except very narrowly along the lake shore.

On Sesse the outcome was much more decisive. Situtunga were found everywhere in numbers which are extraordinary for an antelope accounted "rare" and a denizen only of marshes. They were even more numerous in the overgrown plantations and village sites on the plateaus, and elsewhere on the higher levels, than in the woodland and marshes along shore. The island is nearly forty miles in length, and eventually was explored from end to end. Practically every bit of woodland or jungle upon it was found to be infested by *Glossina*, including points in the interior of the western peninsula known as Buninga that are at least 2½ miles from the lake. The only exceptions were certain areas of woodland in the central portion of the eastern half of the island (Bugalla) which, though hardly a thousand yards from the lake, were completely surrounded by open grass land. Elsewhere a great diversity of inland environment was found, high hills and low; marshes and rocky summits; original forest and the frequently impenetrable jungles which have sprung up in the abandoned plantations; but everywhere that shelter at all attractive to the flies was found, there would be both situtunga and fly.

Except at the very beginning formal records of "catches" in the interior were not kept, because the work of exploration was done almost entirely on dull days or at hours (after 3 p.m.) when the flies are not as active as earlier. The records made at the beginning are presented in Table XVIII, in comparison with those from Bukassa, where inland extension of range is due to great numbers of pigs.

TABLE XVIII.

Catches of Fly on Islands of Bukassa and Sesse (Bugalla) showing Inland Extension of Range due to Presence of Game, made in September 1914.

Collection Points.	Bukassa Island.		Bugalla Island.	
	Male density.	Female ratio.	Male density.	Female ratio.
Lake shore	9·8	10·1 %	24·2	22·5 %
Sandy plain, 400 yards inland	—	—	25·0	16·6 %
Hills, 1,000 to 2,000 yards inland	2·2	10·0 %	10·0	7·5 %
,, 2,000 ,, 3,000 ,, ,, ...	—	—	4·7	9·4 %
,, 3,000 ,, 4,000 ,, ,, ...	—	—	1·3	None Caught.
,, 4,000 or more ,, ,, ...	—	—	·4	

Of significance is the low percentage of females in the interior points; indicating attractive shelter or ample food supply or both.

The only other host animal occurring on the islands, that is found at all commonly more than a few yards from the water front during hours when flies are active, is the monitor lizard (*Varanus*).* On certain islands—notably Manene and Dziru,

* Except on the sudd-surrounded islands of Baujako and Binga, where bush-buck, bush-pig and buffalo occur, and which are faunistically a part of the mainland.

both of very small size—it is extremely common, and on the island of Mbugwe it is far more numerous inland than is usual. On these islands, also, unusual extension of inland range of fly was noted, as described more in detail in Sect. V (*d*) following.

At the end of the island survey the conclusion was definitely reached that the range of fly inland up to a distance of approximately $2\frac{1}{2}$ miles is controlled in the islands by the abundance of food. A summary of observations on this point in tsetse bionomics is presented in Table XIX.

TABLE XIX.

Fly Survey of Islands in Victoria Nyanza showing Correlation between Abundance of Host Animals and Infestation by Glossina palpalis *in the Interior.*

Island.	Infestation by Fly.		Host Animals in Interior.		
	Shore.	Interior	Pig.	Situtunga.	Varanus.
Wema	Heavy	None	None	None	Few.
Kome	Light	,,	,,	Very few.	Very few.
Bugabu	Light	,,	,,	,, ,,	Few.
Bubembe	Light	,,	,,	Few	,,
Bugovu	Light	,,	,,	Very few.	,,
Buvumira	Light	,,	,,	,, ,,	,,
Fumbe	Light	,,	,,	Few	,,
Bunyama	Light	,,	,,	Very few.	Very few.
Lulamba	Light	,,	Very few.	None	Few.
Buvu.	Medium	,,	,, ,,	,,	,,
Bukone	Light	,,	,, ,,	,,	,,
Serinya	Medium	,,	,, ,,	,,	,,
Kitobo	Medium	,,	None	,,	,,
Bukana	Light	Light	Many	,,	,,
Damba	Heavy	Medium	None	Many	,,
Zinga	Very heavy	Light	,,	,,	,,
Sesse (Bugalla):—					
Western Portion	Heavy	Light	,,	Very many	,,
Northern ,,	Heavy	Medium	,,	,, ,,	,,
North Central Portion	Medium	Light	,,	,, ,,	,,
South ,, ,,	Medium	Light	,,	,, ,,	,,
Southern Portion	Heavy	Medium	,,	,, ,,	,,
Mbugwe	Medium	Medium	,,	Very few.	Many.
Manene*	Medium	Medium	,,	,, ,,	Very many.
Dziru*	Light	Light	,,	None	Many.

* Manene and Dziru are small islands less than 1,000 yards in short diameter, but are remarkable in that infestation of the interior is equally as heavy in the case of Dziru and heavier in the case of Manene than along the shore.

V (*d*). Inland Range of Fly as affected by Varanus on the Islands.

Manene Island.

Manene Island is, perhaps, 1,000 yards in length by 500 in breadth. Its northern half is elevated and rocky, its southern half low and fertile. Mostly it is covered with thick bush or forest, except for the rockiest places, and also excepting the site of old plantations in the very middle of the southern half, which are kept open and closely grazed by hippopotamus. These spaces are entirely surrounded by thick bush or forest.

Varanus was more common than on any island of similar size visited. Perhaps as many as six per hour were flushed during the survey of it. They were everywhere, but were especially common in the clear space above-mentioned, where many had their burrows.

There were several bits of sand or gravel beach which offered good breeding grounds and excellent shelter for fly, but the shelter in these was less attractive than that in the close-cropped clearings, surrounded by forest, bush or jungle and with bits of massed vegetation breaking the openings everywhere

The catch of fly was as follows :

	Male Density.	Female Percentage.
Shore points	12·3	21·7
Inland clearing	21·0	1·8

This is quite an exceptional case of concentration of fly away from the water (150 to 200 yards), due to more attractive shelter and constant abundance of food. No breeding places could be found except on the water front.

Dziru Island.

Conditions generally similar to those on Manene, except that shelter in the interior was not so attractive and concentration of fly less notable.

Mbugwe Island.

Mbugwe Island is about two miles in length by one in greatest breadth. It is densely forested, and appears never to have been cleared for cultivation except at a few points, now overgrown with jungle. The one open space discovered on the island is on the crest of a steep hill that occupies the centre of the broadest portion. The very summit of the hill is flat rock, partly covered with thin soil, rank grass and scattered bush. The shore is generally rocky with here and there bits of beach.

Varanus is common. Ordinarily this reptile occupies burrows in rocky places or excavated in light soil in grassy openings, near which are located its habitual basking spots. On Mbugwe there are no such openings as are frequented by it—at least none were seen—except on the crest of the hill above-mentioned, the slopes of which to the very edge of the water were covered with dense, old forest. Hence, although this opening was fully 800 to 1,200 yards from the water, it was much frequented by the animals, which had fairly covered the soil in places with their excreta (containing shells of crabs and molluscs from the lake).

The catches of fly made on this island (4th and 5th March 1915) were as follows :—

	Catch.	Male Density.	Female Percentage.
Points on shore	187	16·6	33·5
Crest of hill	83	13·7	50·6

Breeding grounds were sought for and found in and near the basking spots of *Varanus*, in dry vegetable debris that partly covered the rocks. Six boys, searching for one hour found :

	Total.	Per Boy Hour.
Empty shells	55	9·2
Healthy puparia	21	3·5

The shells had all hatched, and none had been eaten or destroyed by small predators.

This particular colony is the one and only inland infestation discovered at any point which appeared to be quite independent of colonies on shore, and this is the only occasion on which breeding grounds adequate to sustain an independent colony have been found except in old or recent deposits of beach sand or gravel.

The conditions are unique in many respects. The very dense forest which clothed the slopes of the hill was a strong deterrent to dispersions of fly. The local environment was far from being attractive, and it is exceedingly doubtful if the flies would have remained in it if the thick forest had not been so relatively less attractive. But they were walled in as on an island, or as in a great breeding cage—it chanced that there was a regular supply of food—it chanced that there was protection for the pupae—and in consequence the flies remained and bred.

There is no reason why such colonies should not be found at any distance from the water front, except that such conditions are exceedingly rare in this region.

V (*e*). **Dispersion of Fly inland from the Mainland Shore.**

At numerous points on the mainland it was ascertained that inland dispersion of fly was no more extensive than is usual on the islands. The two notable exceptions follow.

Dumo Point, Buddu, June 1915.

Dumo Point is a peninsula with a hill and old plantations, separated from the mainland by an open plain. It is in large part dense jungle. Near the very centre, about 500 yards from the lake shore on two or three sides was a semi-open space, kept grazed by hippo, in which grew great quantities of guava. Bush-buck was rather common. A herd of bush-pig had a retreat in the jungle, and clearly marked trails showed where it made regular rounds of the guava thickets for the fallen fruit. In the immediate vicinity of this thicket, but not elsewhere except in the usual narrow belt along shore, *Glossina* was common. The catches stand as follows:

	Male Density.	Female Percentage.
Points along shore of peninsula	11·6	61·2
At guava thicket, 500 yards inland	8·8	21·4

The shelter at this point was quite attractive, but no more so than at many other points; the inland dispersion of fly was distinctly unusual and the presence of both bush-buck and bush-pig, the latter particularly, led to the conclusion that the presence of fly was thus explained.

Bujaju Peninsula, July-August 1915.

Bujaju Peninsula is an extensive tract of land, almost an island, but with the deep bays behind it choked permanently with sudd. Its shore is very marshy, and principally fringed with papyrus; but inside the papyrus are open spaces, with occasional bits of sandy soil, or traces of old beach line, and these are sparsely infested by tsetse. The interior is much of it "impenetrable" jungle, cut with great numbers of hippo trails, and with clearings, closely cropped by hippo, where once were villages and plantations. Not far from the northern extremity are natural clearings, with very short grass and flat outcropping ledges of rock, and where the soil is sufficient, exceedingly dense clumps and thickets of bushes and vines.

Everywhere on the peninsula the inland range of fly appeared to be normal, except in these natural clearings, which extended a mile or more and were distant 800 to 1,200 yards from the water. Catches were attempted in the clearings kept open by hippo, but without result, or only straggling flies were caught ; but in the natural clearings the greatest density of fly was found of any point on the peninsula. The records are

	Male Density.		Female Percentage.
Points along shore of peninsula opposite clearings	5·9	..	42·3
Point nearest clearing on foreshore	9·0	..	51·1
In clear space kept open by hippo 100 yards inland opposite natural clearings	9·5	..	15·5
In hippo trail leading to clearing 400 yards inland	10·0	..	12·0
In clearing. 800 to 1,000 yards inland	11·0	..	17·5
In open space 300 to 1,500 yards beyond clearing	nil	..	—

Breeding grounds were sought but not found ; but this is no proof that they may not have existed. The shelter was of a most attractive type, but no more so than in other clearings, kept open by hippo, where the soil was much deeper and the vegetation more luxuriant. The only explanation for the presence of fly in such unusual numbers—for, in fact, the major concentration of fly on the peninsula so far as the survey of it extended—was the excellent shelter (probably coupled with breeding grounds) and rather unusual numbers of bush-buck, which appeared to be virtually the only source of food. It was less the numbers, however, than the easy accessibility of these animals which was conceived to be mainly responsible. They found refuge in the dense thickets and clumps of bush, which were so small in extent that the flies could find them at all times without penetrating far into the shadow.

Kitebo Peninsula, August 1915.

Kitebo Peninsula in the district of Mawakota, is bounded by permanent sudd fields, except for a reach of about 3 miles along its south-eastern and southern shore. Here it is narrowly-fringed with sudd of more recent growth and less permanently lodged, which in 1915 was broken at three points. Each break was the centre of a colony, or centre of infestation, for the space between the breaks and on either side of the semi-open reach.

To the northward, behind the permanent sudd fields that fill the channel between the peninsula and the island of Bujako, infestation falls away abruptly. To the westward, behind the permanent sudd fields that bind the western shore and south-western extremity of the peninsula a curious situation was discovered.

The south-western extremity of the peninsula is a marshy plain with belts and patches of drier land. The wetter parts of it are overgrown with a terrible tangle of tall grass, shrubbery and briery vines that defies penetration. The drier parts are in places open game pasture, and in part covered with patches of dense jungle.

The whole area forms a triangle, with its base against the higher ground (densely forested) and its apex lost in the tangled mass of vegetation that stretches outwards into the sudd.

Crossing this area, some distance from and very roughly parallel to the forested base of it, is a sandy ridge, densely overgrown with shrubbery and jungle. The tangled marsh is beyond this ridge, and inside it are the game pastures, very closely cropped by hippo and bush-buck. (Hippo crop almost as closely as sheep, using their horny-edged lips.) The ridge is an ancient beach line and affords fair breeding grounds and adequate shelter, which is supplemented by the patches of jungle scattered over the game pasture.

In addition to bush-buck, which were unusually common, were plenty of more or less recent tracks of water-buck, bush-pig and buffalo, which came out from the forest, and from other game pastures 2,000 to 3,000 yards through the forest.

The infestation along the ridge was interesting :—

	Catch.	Male Density.	Female Ratio.
At break in sudd, and hippo landing	195	44·5	54·3%
200 yards from open water, on ridge	114	29·0	49·1%
700 ,, ,, ,,	64	20·0	37·5%
1,100 ,, ,, ,,	55	20·0	27·2%
1,500 ,, ,, ,,	17	6·5	23·5%

There could be little doubt, in this case, that the bush-buck were mainly responsible for inland dispersion, for they greatly outnumbered the other game animals; of *Varanus* there was none, of crocodile but few, and the hippo herd slept far away from its nightly pasture.

There was also infestation at open points in the forest at distances believed to be 2,500 yards from the lake, but it was slight and not accurately measured. At the game pastures from 3,000 to 5,000 yards away from the open water—not far from the western sudd field—no fly could be found; water-buck was the principal species grazing in them.

V (*f*). **Dispersion of Fly inland from Lake Shore along small Rivers.**

At various points on the western shore of the Lake, in the district of Buddu, larger streams or creeks than exist on the islands flow into it. One of these, Mujuzi, enters the lake about two miles north of the old canoe landing at Kalkosa, and three miles south of that at Bale. South of the creek all the way to Kalkosa the shore is marshy, with an old beach line overgrown with dense vegetation. At the mouth of the creek an old sand beach begins, at a level of some two to three feet above the present beach line and continues nearly to Bale. The foreshore also is sandy, but except for a reach of 600 to 800 yards just north of the creek, it is overgrown with dense vegetation of an impenetrable character to the water's edge.

At the mouth of the creek the breeding grounds and shelter are of the best, and food is provided by a large number of crocodiles which find harbour there, and which also rest in the sand. To the north there is some breeding ground, but shelter is repulsive and no indication of any sort of food was seen. To the south there are situtunga and perhaps other host animals, but shelter is repulsive and no breeding grounds were seen. Conditions of life at the very mouth of the creek, over a radius of hardly more than 50 yards, are highly favourable for tsetse, but favourable conditions are extremely localised, making for a sharply defined colony that fuses with a small colony at Kalkosa landing (point 40 in Fig. 5), to the southward, but tapers away to a minimum of ·5 at Bale (about 1,200 yards beyond point 53), where a colony yet further north fuses narrowly with it.

Mujuzi Creek is almost a river, being at points some 10 yards in width and of considerable depth. Its shores are thickly wooded, and cannot well be followed because of the tangled vegetation. There are occasional pools with low sand bars, as at points 45C and 45D. The stream was quite open as far as point 45E, where it was choked with floating vegetation which extended for a considerable distance. At points beyond 45F it was open again, and at one point ran through a tract of woodland which seemed the headquarters of a herd of buffalo, but beyond point 45F, which was approximately 2 miles from its mouth, no fly was seen. At no point from the mouth inland was shelter especially attractive; no breeding grounds were seen, and host animals were certainly not abundant.

If allowance is made for the general attractiveness of the shelter from point 45 to beyond point 46 along the lake shore, the falling off in density of fly appears to be approximately the same on the lake shore northward to Bale, and along the creek inland. It is more pronounced along the creek, but not very much more. The conditions of life are unfavourable to tsetse in all three directions from the colony centre, and infestations of the creek banks and lake shore alike for a distance of from two to three miles is plainly due to the existence of exceptionally favourable conditions in the extremely limited space around the mouth of the creek.

Extension of range inland along other creeks wide enough to create something of an alley-way through the bush or forest for the moving flies to follow has been found to be much as in this instance.* The flies follow the waterways much as they follow the lake shore. But as yet no colony centre, or semblance of such comparable to the hill colony on Mbugwe Island (Sect. V (*d*)) or the inland colony in Bujaju (Sect. V (*e*)) has been discovered on the banks of any stream.

Every bit of evidence that has been gathered supports this final conclusion concerning the range of fly inland from the lake shore; it is primarily controlled by the distribution of host animals, and there is nothing to indicate that this tsetse requires open water or humid conditions, or that water is even attractive to it. Its favoured hosts are amphibious in habit; the most attractive types of shelter occur more commonly near the shore than inland; and it rarely finds good breeding places elsewhere.

It may be added that every instance in which fly was encountered other than as mere stragglers at a distance greater than 500 yards from the lake shore has been covered in this section.

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* If the stream is so small that no break is caused in the continuity of the forest, fly has not been observed to follow it.

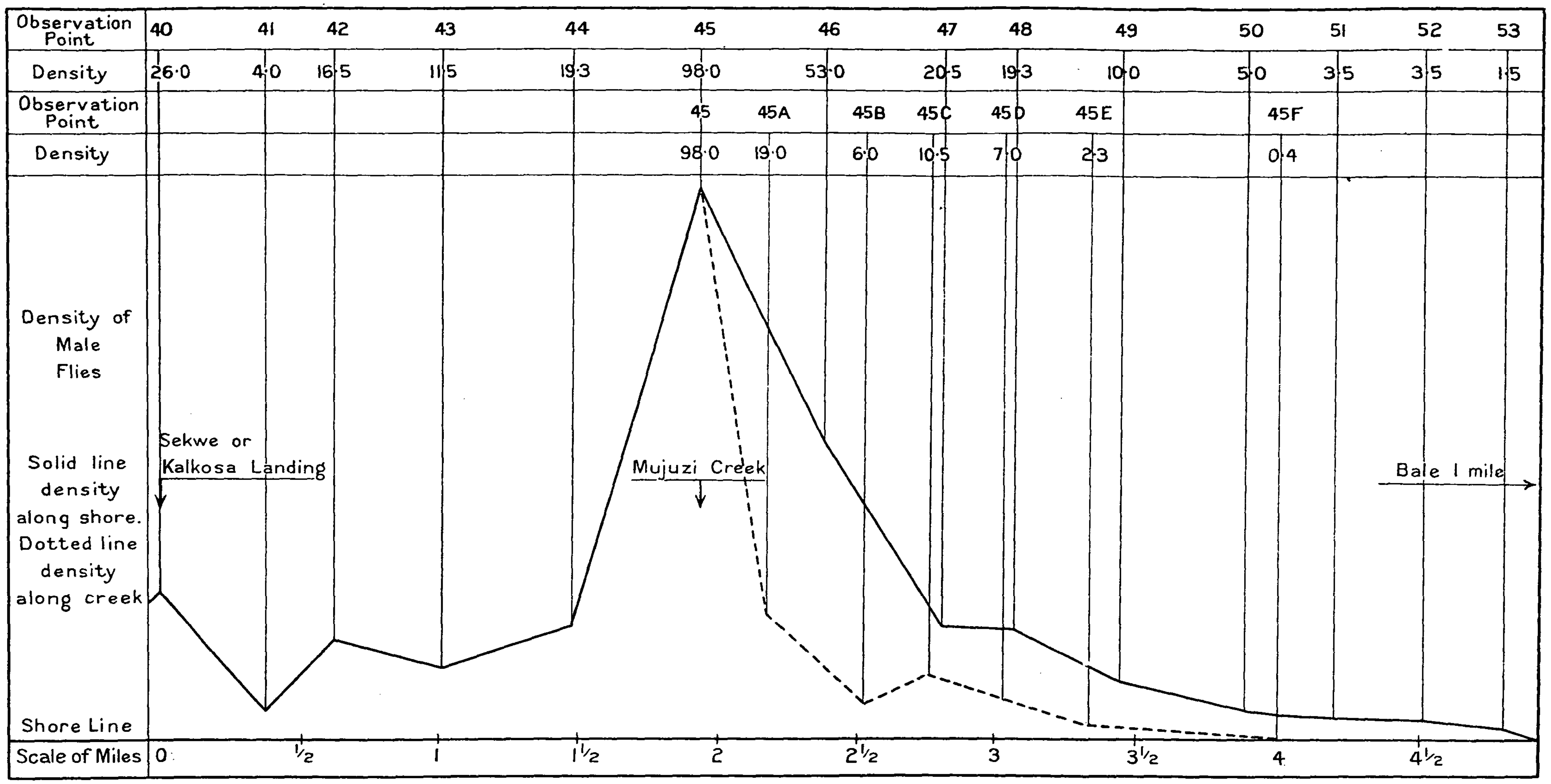

Fig. 5. Fly survey of mainland shore from Kalkosa to Bale, Buddu, showing inland spread of fly on Mujuzi Creek.

V (*g*). **The Sex Ratio at Points where Range is extended inland.**

In the records of catches at inland points which have been given in the preceding paragraphs a very significant feature is the falling off of female percentage coincidently with the falling off of male density, as distance from the water point increases.

This is notable in the catches on Bugalla Island (Table XVIII), at Dumo Point, on Bujaju Peninsula, and on Kitebo Peninsula (Sect. V (*e*)). On Bujaju and also on Manene Island the male density was greater inland, but the female percentage strikingly lower. On Bukassa Island male density fell and female percentage remained the same, with no serious exception. The Mbugwe hill-top colony is the one striking exception, and this is also unique in being, apparently, quite independent of colonies along the shore and entirely different in this respect from the infestations at Dumo, Bujaju, Kitebo and on Bugalla Island, which are extensions inland of shore colonies.

This same phenomenon has been noted repeatedly at other points on Bugalla Island, where collections were made at distances of 500 to 2,000 yards inland, and the whole series of observations falling into this category stand in the sharpest contrast to the rule that applies along shore (so well illustrated by the curves in figure 4, p. 372) that female percentage rises as the distance from the centre of infestation increases and male density decreases. And it stands, perhaps as the best bit of other than purely empirical evidence, in proof of the effect of food supply or distribution of host animals upon inland range of fly.

The shelter on Bugalla Island, for example, or at Kitebo, is in every respect as good and attractive to the flies as on the foreshore. Food is better, and more abundant. It is only the protection afforded by the breeding grounds that is lacking to make the inland conditions of life entirely favourable.

TABLE XX.

Mujuzi Colony. Dispersion forced, by hunger, into an intolerable environment.			Kitebo Colony. Dispersion induced (inland) by superior attraction of environment.		
Distance of observation point from colony centre.	Male density.	Female percentage.	Distance of observation point from colony centre.	Male density.	Female percentage.
0 yards	98·0	45 3	0 yards	44·5	54·3
700 „	53·0	49·2	200 „	29·0	49 1
1,300 „	20·5	64·0	700 „	20 0	37·5
1,700 „	19·3	72·7	1100 „	20·0	27·2
2,300 „	10·0	80·8	1500 „	6·5	23·5
2,900 „	5·0	88·8			

The fly cannot breed inland, and hold its own numerically, on account of lack of good breeding places; but there is continual inland dispersion of flies from the colony centres at the breeding places on the foreshore, induced by relatively better or more food and equally attractive shelter. The flies are drawn away from the colony centre, or centres of infestation, by more attractive conditions elsewhere. In the colony at Lutoboka Bay (fig. 4) or at Mujuzi Creek (Sect. III (*e*)) dispersion is, on the other hand, forced, and the flies, instead of being drawn outward by a superior attraction, are forced outwards into a relatively repulsive or intolerable environment by the stimulus of hunger. In this latter case female percentage tends to soar as male density falls; in the former male density and female percentage fall together, as shown in Table XX. And it is certainly superior food in combination with equally attractive shelter which explains inland dispersion in all the cases that have come under observation, except inland from the lake along the banks of the Mujuzi and a few other creeks, which is comparable to dispersion along the shore of the lake.

VI. Hosts and Host Preferences of Glossina Palpalis.

VI (*a*). Methods of Studying Hosts and Host Preferences.

These methods were used for the study of hosts and host preferences of *Glossina palpalis* :—

(1) Experiment. The animals were tethered along fly-infested shore (see Sect. VI (*c*)).

(2) Approach and observation. Wild and domestic animals were approached and the behaviour of fly toward them was observed under entirely natural conditions (see Sect. VI (*d*)).

(3) Shooting. When possible, wild animals were shot in the fly belt at hours when flies were active. If the animal falls without running the flies which have been following may linger by it for a time, and some of them will usually feed (see Sect. VI (*e*)).

In addition to the above the study of sex ratio, as affected by the density of favoured hosts, affords an opportunity for securing supplementary or confirmatory data (see Sect. V (*g*)).

A list of the principal animals that occur within the fly belt, together with methods by which they were studied as hosts of fly, and a summary of conclusions reached is presented in Table XXI. The list excludes many small mammals, such as rats, bats, etc., which though common are certainly of no importance as hosts of fly, and it also excludes others such as *Hyrax*, the "edible rat," and others which are rare or nocturnal and of no importance, in this region at least.

All animals which are fed upon by *Glossina*, and thus technically included amongst its hosts, are not equally favoured or preferred by it, and a broad line of distinction may be drawn between the two following categories :—

(A). Hosts which are positively attractive and which are favoured or preferred to such an extent as to cause concentration of fly in localities that they frequent.

(B). Hosts which are rather repulsive than attractive and which are avoided to such an extent that the flies tend to scatter and disperse from localities in which no more favoured hosts occur.

In numerous cases there is no doubt into which category an animal falls, and such are designated by an exclamation point (!) in the table. In other cases there is considerable doubt. These are indicated by an interrogation point (?). In one or two, notably that of the domestic ox (see Sect. VI (*c*), Experiment 3), some individual animals appear to be attractive and others repulsive.

There are two tests for distinguishing between attractive and repulsive hosts :—

(1) An attractive host is apt to collect a "following swarm" of fly. This curious phenomenon is associated with the assembling of the sexes and is described in Sect. IV.

(2) The range of fly—especially its range inland from the shore—is likely to be notably extended through the presence of favoured hosts. This phenomenon is discussed in Sect. V.

TABLE XXI.

Summary of Observations on Hosts and Host-Preference of Glossina palpalis *on Victoria Nyanza in Uganda.*

Animals observed in fly belts.	Methods of Study.			Conclusions.		
	Experiment.	Approach and observation.	Shooting.	Is animal fed upon?	Is animal a favoured host?	Is range of fly affected by animal?
Crocodile	Yes	Yes	Yes	Yes!	Yes!	Yes.
Varanus	Yes	Yes	Yes	Yes!	Yes!	Yes.
Tortoise	No	Yes	No	Yes	Yes	No.
Serpents	No	Yes	No	No?	No	No.
Lizards	No	Yes	No	No?	No!	No.
Situtunga	No	Yes	Yes	Yes!	Yes	Yes.
Hippo	No	No	Yes	Yes	Yes	Yes?
Bush-buck	No	No	Yes	No??	No?	Yes??
Bush-pig	No	No	Yes	No??	No?	Yes??
Water-buck	No	No	Yes	No??	No?	No?
Buffalo	No	No	No	O	O	No?
Duiker	No	No	No	O	O	No.
Zebra	No	No	No	O	O	No.
Wart-hog	No	No	No	O	O	No.
Reed-buck	No	No	No	O	O	No.
Monkeys	No	Yes	Yes	No?	No!	No.
Otter	No	Yes	Yes	No?	No!	No.
Mongoose	No	Yes	No	No?	No!	No.
Hyaena	No	No	No	O	O	No.
Leopard	No	No	No	O	O	No.
Birds	No	Yes	No	No?	No!	No!
Man	Yes	Yes	No	Yes!	No!	Yes.*
Ox	Yes	Yes	No	Yes	Yes?	No?
Pig	Yes	No	Yes	Yes	Yes	Yes.
Goat	Yes	Yes	No	Yes	No!	No.
Sheep	Yes	No	No	Yes	No!	No.
Dog	Yes	No	No	Yes	No!	No.

* Human presence affects range of fly negatively.

O. No evidence either way: animals rare or uncommonly seen by day.

It is important to know into which category any given host species falls, if squarely in either. It is certain that a repulsive host will not attract a "following swarm," and notes on observations of such swarms in association with any particular host are valuable in doubtful cases.

There are two host species, crocodile and *Varanus*, which form, apparently by themselves, a category of most favoured hosts. They are not only most attractive to fly, but the most favoured and best protected breeding grounds of the fly are frequently identical with either (*a*) spots selected by crocodiles as its own breeding grounds, or (*b*) spots selected by *Varanus* as a basking ground. (The female crocodiles habitually frequent their breeding grounds, and bask over the spot where their eggs are buried.)

On this account *Glossina palpalis* becomes something like a specific parasite of these reptiles, suggesting not distantly those domiciliary parasites that do not live on the body but in the nests or domiciles of their hosts, and which are specifically adapted to such a mode of life.

VI (*b*). **The Habits and Habitats of the Hosts of** *Glossina palpalis* **in the Region of Victoria Nyanza.**

The following very general notes and observations are drawn up with the idea of indicating the practicability of controlling the fly through extermination of its hosts. No proposition of this character should be considered, however, without also considering the data presented in Sect. II (*d*).

Crocodile.

Crocodile is undoubtedly the most important host of *Glossina palpalis* in this region. It is common nearly everywhere, on islands and mainland alike, and on or off rocky, marshy, clay-banked, sandy and gravelly shores. It is excessively numerous at times along certain reaches of marshy or papyrus-fringed shore (notably on certain floating islets north of the island of Bunjako where in August 1915 dozens and scores were seen basking together), but it cannot breed in such places. These are its feeding grounds, and individuals frequenting them must go, in some cases considerable distances, in search of the sandy or gravelly places in which alone they deposit their eggs. Much frequented breeding grounds were found—notably on the mainland in that district of Buddu known as the Swamba, and on certain islets, notably that known as Dwavannu, which lies just off the southern tip of Luambu Island, where nearly a score of occupied "nests" were found in July 1915.

The females brood daily for long periods over the precise spot where their eggs lie buried, and at such times are especially exposed to attack by *Glossina*, and provide for it a regular supply of food.

Neither breeding nor basking spots are very far from the shore; perhaps never more than 100 and rarely more than 50 yards. In consequence inland range of the fly is not affected by this host, as it may be by *Varanus*.

If it were deemed desirable to reduce the numbers of these reptiles, it could probably be done by placing a small bounty on their eggs or by locating all the favoured breeding places and making regular rounds of egg destruction. In German East Africa, I was informed, a bounty had been placed on eggs as a measure for reducing the density of *Glossina*. But such measures, to be really effective, ought to include the lake as a whole, for the animals undoubtedly move about considerably in search of feeding and breeding grounds.

They are not ordinarily hunted by the natives, who make no use of either flesh or skin, and who, though they detest the animals, will not take the trouble to destroy their eggs when found. Depopulation, the natives assert, has had no effect on the numbers of crocodile infesting the islands. They are probably almost unmitigated vermin.

Varanus.

Varanus, or the monitor lizard, is second only to the crocodile in importance as a host for *Glossina palpalis*. It is distributed on and near the rocky shores of islands and mainland. It is much more at home on land than the crocodile, and may wander so freely and to such considerable distances inland as to affect the range of the fly notably (see Sect. V (*d*)).

Few animals enjoy a greater diversity of purely animal food. Its excreta, sometimes abundant in much-frequented basking grounds, show it to feed largely on molluscs, both terrestrial and aquatic, and very freely on the fresh-water crabs that often abound under stones in shallow water. An abundance of crabs is sure to attract great numbers of *Varanus*, and nearly always, except on small and poorly sheltered islets, an abundance of *Varanus* is correlated with abundance of tsetse. But the reptile also feeds freely on insects, both aquatic and terrestrial, including among the latter such unsavoury types as cockroaches and scavenger beetles; fish and other small vertebrates, including certainly snakes and frogs; the eggs of birds, and also (so it is said) eggs of crocodile.

It domiciles itself in burrows which it excavates in sandy soil, in crevices of rocks and, quite commonly, in termite nests. Usually there is a well marked basking spot near at hand, and there occur quite frequently the breeding places of tsetse.

Its own breeding places are variously described, and declared by some European observers, positively, to be in old termite nests. But it appears more probable that they are in large mounds of earth and debris thrown up by the animals, but not watched over by them. These curious mounds are common, but of those excavated none were found occupied. The tsetse is only by chance associated with its host at these (assumed) breeding places, and there is no coincidence between the location of them and the haunts or breeding places of fly.

On certain islands and islets, notably Manene and Dziru, *Varanus* was found so commonly that an average of four or five would be flushed per hour of hunting. Such abundance, the natives assert, was unheard of previous to the depopulation of the islands, and undoubtedly the species has increased notably, and the tsetse with it. They are so eagerly hunted by the natives, partly for their flesh, but especially for their skins, that their numbers would certainly be reduced if the islands were repopulated. The skins are so highly prized—for making musical instruments—that it is doubtful if any reward or bounty would lead to the destruction of much larger numbers.

Tortoise.

No species of tortoise (or of turtle) is at all commonly encountered in this region. Therefore, though tortoise is freely fed upon and apparently a favoured host it is of insignificant account in this particular region. Elsewhere it might be of prime importance as a factor in *Glossina* bionomics.

Serpents.

Serpents are not commonly encountered, except, perhaps, on a few islets (notably Tavu, where a cobra was unusually numerous) and on certain sandy plains much frequented by a small earth-coloured snake. Of those observed, a python and a puff-adder seemed most likely to serve as hosts of tsetse, but both were so infrequently seen that no python and only one adder was observed in a fly-infested locality at hours when the flies were active.

In view of the notable proclivity of this tsetse to feed on reptiles, it pretty certainly attacks serpents, but in this region they cannot be of any consequence as hosts.

Small Lizards.

Small lizards of several species are very numerous in fly-infested localities, but all evidence that they are ever fed upon is negative. Certainly they are of no importance as hosts.

Situtunga.

Although usually accounted a rare species, this antelope is easily third in importance among the hosts of *Glossina palpalis* in the region under consideration. On the mainland its range is restricted by the leopard or human hunters to marshy areas, either forested or overgrown with reeds, grass or papyrus, and to a zone of varying width (maximum observed about 2 miles) surrounding these protected areas.

It is possibly unique (together with other " species " of its subgenus) amongst antelopes in that it swims well and takes voluntarily to the water. This permits it to occupy islands where no other antelope occurs, and it is the only species occurring on any of the islands visited, except those of the Mawakota group (Bunjako, Binga and perhaps Bussi and Zinga), which lie near the western shore of the lake, and are connected with the mainland by fields of floating sudd.

Except on these sudd-bound islands there are no leopards on any that have been visited. Previous to the removal of the island population, in 1909, the antelope was restricted in insular range to the uninhabited islands of Nkose and Mwanse, and to the larger inhabited islands upon which large areas of marshy land afforded the protection required against leopard and human hunter alike. But following depopulation it was free from destructive enemies and not only multiplied with remarkable rapidity on the islands it formerly occupied (*i.e.*, those with large marshy areas), but extended its range to other islets and islands hitherto free from it.*

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* The following notes were made on distributions in 1915 :—

Damba Island. Originally infested, now densely infested.

Kome Island. Originally infested, now lightly infested. Spread (since 1909) from Kome to Namba and Nsadzi Islands.

Bugalla-Buninga (Sesse) Island. Originally infested, now very densely infested. Spread (since 1909) from Sesse to Fumve, Bubembe, Bunyama, Manene, Bufumira, Bugaba and Mbugwe Islands.

Nkose Island. Originally and still densely infested.

Luambu Island. Newly infested from mainland.

Bunjako, Binga, Zinga, Bussi and other sudd-bound islands all originally infested.

On these islands it has forsaken the unnecessary protection of the marshes, and assumed habits much more like those of the bush-buck on the mainland. It is most common in the jungles which have sprung up in the abandoned plantations and village sites, and is generally more common on the highlands than in its original habitat. At points it has browsed on shrubbery growing on precipitous rocky slopes which would seem to afford it the scantiest foothold. Its elongate hoofs spread so easily as not to impede rapid flight, if alarmed, even on rocky soil, and they are also worn away nearly to the length that is normal for animals that frequent rocky places.

It has developed into a most destructive enemy of many species of plants. Some of its most favoured food-plants, formerly very common, have been virtually exterminated over wide areas. There is one plant, allied to the cultivated canna, which was perhaps the most common and conspicuous of any forest herb. It formerly covered the forest floor over extensive areas on Sesse Island, growing to a height of 2 to 7 feet, and effectually concealing and protecting (in a crouching position) the antelope that fed upon it. Hundreds of acres were covered with this plant to this degree of density in the autumn of 1914, but a year later the plants had been browsed to the roots nearly everywhere. Of one species of woodland shrub, formerly very common, not a living shoot could be found in 1915. Of many species of trees, vines and large shrubs not a living seedling, leaf or young shoot within reach of the animals could be found. Areas formerly thickly massed with fern had been browsed to the bare earth and roots. And when trees fell in the forest it happened repeatedly that the animals prevented other trees from springing up, and the spaces thus became open glades.

The animals on Sesse Island were rather badly afflicted as they grew older with a mange or " scab " parasite, which seemed to be causing more trouble in 1915 than in 1914. On Damba Island this parasite did not occur. It appeared possible that it might prevent much further increase on Sesse. If not, and if nothing else disastrous supervenes, the animal must speedily adapt itself to the grazing habit, for it had reached and passed far beyond the maximum density which the island would sustain if it retained its woodland habit of browsing.

This " outbreak " of situtunga presents so many points of interest that it was carefully studied as a legitimate phase of these investigations, and much more was learned of it than can well be included here.

The effect on the range of *Glossina* of the increasing numbers of situtunga has been already described in Sect. V (*c*). The further effects are bound to be profound if increase continues. There are certain islands (notably Bunyama) where density of fly was well below the average in 1914–15, but where conditions are very favourable to rapid increase of the very small herds of situtunga then domiciled upon them, and also such as to make spectacular increase in density of fly almost a certainty if the antelope increases.

The animal is assiduously hunted by the natives for flesh, skin and horns. As already noted, they had either exterminated or prevented establishment of the species on islands devoid of the specific protection afforded it by marshy tracts, and, in time, they would pretty certainly exterminate it again if the islands were repopulated. To exterminate it from the great fields of sudd which are permanently anchored in the more protected bays and channels of islands and mainland would doubtfully be possible; nor would it be necessary, for these tracts are beyond the range of tsetse.

It can exist despite beasts of prey and European or native hunters in such natural protection, and requires no additional legal protection to save it from extinction ; and under such conditions it is harmless. But on the islands where leopards are absent, it is absolutely to be classed as vermin wherever a human population exists or may exist.

Hippopotamus.

Hippopotamus is generally distributed and, for an animal of its size, common nearly everywhere on the island and mainland shores. It stands fourth in importance among the hosts of *Glossina*, but is of much less importance than its numbers might imply, because of its habits. There are isolated individuals and small herds (herds of more than 15 or 20 are rarely encountered) which habitually sleep on land or with their bodies partly exposed along shore during the hours of activity of the fly, but these comprise only a small minority of the animals in this region. Those composing the large majority habitually sleep in deep water, and are very rarely seen on land or near enough to it to be reached by the fly during hours of its greater activity.

In a very few cases, where herds or individuals habitually repaired to some small islet or isolated peninsula to sleep by day, the density of tsetse appeared to be greater than would otherwise have been expected. But it is improbable that the effect of the extermination of this animal on range and density of fly could be easily measured or appreciated. At all events it is only those particular individuals or herds that sleep on or close to shore which are of any account in this connection.

The animals have not increased in numbers according to some natives, and have done so according to others, as a result of depopulation. They were formerly hunted, not very successfully, for flesh and skin, and also as pests, for they may be terribly destructive to plantations. On many islands it was necessary to protect plantations from their ravages by deep ditches on the water side, and sometimes on all sides.

Probably the most pronounced effect produced by the presence and activities of these animals on *Glossina* is that they keep open and closely cropped considerable spaces on shore, especially in the old plantations. These open spaces or grazing grounds are sometimes two miles or more inland, with hard beaten trails leading to landing places on shore. They are also favoured haunts of situtunga on the islands and of bush-buck on the mainland, and since they are usually in localities where the soil is fertile, they are generally banked about with thickly massed vegetation which affords ideal shelter for tsetse. Many points along shore, or inland on the islands overrun with pig, situtunga or *Varanus*, are thus made attractive to tsetse, which would otherwise be covered with vegetation of an unattractive or positively repulsive type.

Bush-buck.

Bush-buck is common nearly everywhere along the mainland shore and on the sudd-bound islands of Bunjako and Binga. It is by its habits and habitat much less suitable than the situtunga as a host for tsetse, for its best natural protection is found in the thick tangles of shrubbery and vines that grow in dry and rocky places where sylvan or jungly vegetation will not flourish.

Evidence concerning its status as a host of tsetse is conflicting ; possibly it is to be ranked fifth in importance of the wild hosts in the general region.

It is hunted by the natives, but less assiduously than situtunga, and is the most persistent of the antelopes, except situtunga, found in this region. It is said to have increased considerably in the depopulated belt ; certainly it has found favourable conditions of life in many of the deserted plantations and village sites along shore.

Bush-pig.

The bush-pig ranges with bush-buck and is about equally common. Its preferred habitat is the jungles that grows in marshes which are not too wet, or on hills which are not too dry, and which are its natural protection against leopard. It is by its habitat no very suitable host for tsetse, but it may tie with bush-buck for the position of fifth in relative importance.

It is assiduously hunted by the natives, both for its flesh, and as a major pest of plantations. It is properly classed as vermin from every point of view, but as long as its natural protection is provided, it will doubtless defy native and European hunters, and beasts of prey alike successfully.

The natives aver that its numbers have increased notably as a result of depopulation.

Water-buck.

There is no water-buck on any island, but at certain points on the mainland it has become very common as a result of depopulation. No evidence associating it with tsetse was secured, but its numbers appear to be increasing rapidly in the depopulated zone and it might easily become a host of some importance.

The natives positively assert that it was formerly unknown in certain localities—the peninsula of Gova especially—where it is now common and increasing.

Zebra.

A few zebra are running with herds of water-buck on Buganga and Kiteba peninsulas. The natives assert (positively) that it was formerly unknown ; in fact, they showed complete scepticism concerning its present existence on the shore, until visually convinced.

Wart-hog.

Wart-hog has come into Buganga peninsula along with zebra and water-buck. The natives assert that it was unknown before depopulation, but it is as yet very rare.

(The return of these animals to territory from which they had been exterminated by the natives illustrates well the effect of native population on game, and indirectly, perhaps on tsetse.)

Reed-buck.

Reed-buck is a rare species in or near the fly belt and finds its best natural protection in vegetation that is positively repulsive to tsetse. It is of no consequence whatever as a host.

Duiker.

A small duiker, of unknown species, was seen in some numbers on the peninsula of Bunjako. Its habits keep it well away from tsetse, so far as observed.

Buffalo.

Numerous herds of buffalo, said to be increasing, range over much of the mainland shore, and others exist on the sudd-bound islands of Binga and Bunjako. The animals come to the shore itself, but the herds keep well together and each ranges over a considerable territory, so that despite the number of animals, they do not afford an at all constant or regular supply of food for tsetse. A herd may remain for several weeks without coming near the shore, and then for a week or two range nowhere but along it.

It is believed that buffalo would be a favoured host of fly if it were less inclined to wander, but no evidence whatever could be secured.

Leopard.

Leopard is of very great importance in the bionomics of tsetse as a deprivative enemy, for it is a major factor in controlling the range and density of bush-buck, situtunga, bush-pig and perhaps other hosts of the fly. As such it is discussed elsewhere.

It is very doubtfully a host itself, for though common enough in the fly belt, it is extremely seclusive by day.

It has probably increased with the game, and its range has been extended since depopulation to include the islands of Bussi and Zinga. Formerly it occurred only on the mainland and the sudd-bound islands of Bunjako and Binga. Bussi and Zinga Islands were not completely sudd-bound, but were separated from the mainland by a narrow open channel, used in canoe traffic. With cessation of this traffic these waterways were allowed to become choked—permanently unless the Government reopens them—and the leopards promptly crossed to the islands. The channel between Bussi Island and the mainland was the first to close, and the leopards crossed and increased to greater numbers (as evidenced by tracks and excreta) than in any other district visited. The channel between Zinga and the mainland was not known to be closed until in August 1915, when excreta of leopard were found on the island—once only seen in some five days spent in fly survey—and on investigations the channel was found choked.

Monkey.

The common *Cercopithecus* ("green" monkey) occurs everywhere in the fly belt on the mainland, and on most of the larger islands. On the islands, in the absence of leopard and man, it is usually much more numerous than on the mainland. It was hunted as a pest by the natives and is said by them to have increased. An impression, not confirmed by actual study, was to the effect that the animals on different islands were developing into fairly well marked local varieties.

The animal appears to be consistently avoided by tsetse, and despite the facts that the flies are known to be pathogenic towards monkeys (of this species) on several of the islands, and that the monkeys forage freely along beaches densely infested by fly, they take no visible harm. Their numbers appear to be limited only by the amount of food available.

Other monkeys occur in the fly belt on the mainland, but they are more strictly arboreal. A lemur occurs on Bunyama and perhaps other islands.

Small Mammals.

Otter is very common on the islands; mongoose on certain islands; "edible rats" on Sesse (Bugalla) and perhaps others; *Hyrax* on Sesse; civet cat on Sesse; rats (in excessive numbers, sometimes) on many islands; and one or two other small mammals were observed. None are of the slightest account as hosts of tsetse, so far as any evidence even remotely indicates.

Fruit bats, including a large "flying fox," are characteristic of the island fauna, on account of the great quantities of wild figs that abound along rocky shores. The smaller species sleep suspended from low bushes in such a manner as to expose themselves to tsetse, but there is no shred of evidence that they are ever fed upon.

Birds.

A very conspicuous feature of the island fauna is the excessive abundance of shore birds: cormorants of two or three species, and darters. They breed in low bush along the shore and roost in great numbers on trees and (frequently) on low rocks, which bring them within easy reach of tsetse. The flies must occasionally feed upon these birds, but every bit of evidence which could be secured was to the effect that they are of no importance whatever as hosts. They outnumber other large birds occurring along the shore.

These others include egret, heron, ibis, crested crane, open-billed stork, saddle-billed stork, whale-headed stork (or shoe-bill—not uncommon in certain environments), Nile goose, spur-wing goose, and a few others which are potential hosts of the fly. But none, apparently, are fed upon except, possibly, in emergency.

Domestic Animals.

Oxen and goats are occasionally to be seen herded on the borders of the fly belt, as at Entebbe. Formerly oxen, goats, sheep and dogs were domesticated by the islanders and, despite constant contact with tsetse, appear to have done very well. There appear to be no cattle ticks on the islands at the present time, and before depopulation not all the disease-bearing ticks were present, according to available evidence. This and the absence of beasts of prey make the islands highly favourable for breeding of live-stock.

Domestic pigs were introduced to the islands by Europeans. A few escaped into the bush and were left when the islands were depopulated. They increased to excessive numbers, which were latterly reduced through unknown causes—possibly superabundance and famine. They have adapted themselves well to wild life, and have habits very suggestive of the bush-pigs (not in the least like wart-hog) on the mainland. But they would fare badly in open competition with the wild pigs, for their efforts to uproot the earth are relatively puny and bush-pigs will secure food where domestic pigs might starve.

On the one island where they occur abundantly (1914–15) they are favoured hosts of the fly, and responsible for its notably wide dispersion, if not greater density. They could doubtfully exist in the wild state in competition with bush-pig and might not be able to escape leopard, but on the islands they thrive so exceedingly well in the bush that they are to be classed as vermin, and ought certainly not to be introduced into any island unless strictly confined.

Sheep and goats are not at all favoured hosts of tsetse; the status of the domestic ox is somewhat doubtful, but probably differs greatly from time to time and place to place.

Man.

Previous to the sleeping sickness epidemic all the larger islands were permanently inhabited, and fishing camps or temporary villages were located in many of the smaller ones. The mainland was also well populated, and temporary fishing villages or camps occupied by fishermen were located on reaches unfit for permanent habitation.

About 1900, the population of Buvuma Island and adjacent parts of the mainland was decimated by famine, accompanied by the outbreaking epidemic of sleeping sickness, which latterly spread into Buganda and the Sesse Islands, to the westward. In 1907 a belt along the mainland shore was evacuated by the natives at the advice of the Government, and two years later the islands were similarly depopulated. Thereafter, except at the lake ports for steamers, which were protected by local clearings, the whole fly belt was a proscribed zone, into which few natives or Europeans were authorised to enter. This zone includes all the islands (except the western shore of Bussi) and a two mile belt along the mainland shore.

Notwithstanding this proscription, man continued to come into measurably broad contact with tsetse-fly. Although the clearing at the open ports reduced density of fly to a perfectly innocuous minimum, they did not exterminate it. With enough patience I could always find tsetse in the Botanic Gardens and at certain other spots in Entebbe. Density was very low—not more than 0·2 or 0·3 by the standard adopted herein for comparative measurement—but considerable portions of Entebbe township lay within the range of the species, and a large population lived in very narrow contact with the fly.

At other open ports, notably at Bukakata, larger portions were included within the fly belt; density of fly was greater, and the local population came into broader contact with it. At Bukakata the population was very small, but it lived very broadly in contact with a not inconsiderable infestation.

Poaching within the proscribed area was, at points on the mainland, rather flagrant, and some of these points were very badly infested. The reach of shore covered by the northern spread of the Mujuzi colony (p. 387), which is the very worst infestation discovered, was, strangely, a favourite haunt of poachers. No less than 22 discarded or hidden fish-traps were found along some two miles of shore. Man was by no means a rare or uncommon host of tsetse at many points covered by the fly survey.

The islands were much less freely visited by poachers, especially after my fly survey was begun, but those nearer the mainland showed many traces of illicit occupation, most of them however old.

Taking the mainland only, man was about as frequent a visitor in the fly belt as water-buck or buffalo.

VI (*c*). **Experiments with Animals under Constraint to determine Host Preferences of** *Glossina palpalis.*

1. *Comparison between Goat, Pig,* Varanus *and Man.*

This experiment was made on Lugazi Island in December 1913. Mention has already been made of it (Sect. II (*b*)). The animals were exposed as equally as possible along a bit of beach. The goats were native stock and full-grown; the pigs of European stock and only about one-quarter grown; the *Varanus* were newly caught, one being full-grown and the other about half.

The bites inflicted upon man were counted for comparative purposes, but the comparison is not exact, because only the flies actually engorging on the animals were counted, and some bit without engorging. The goats appeared to have been bitten several times, and each time prevented the fly from feeding. The complete immunity of goats and man, in so far as engorgement is concerned, is due to the same cause—an instinctive movement in self-protection which causes the fly to desist from attack. Neither were immune from being bitten, and bites on goats were probably about as numerous as on man.

TABLE XXII.

The Relative Attractiveness of Varanus, *Goat, Pig and Man to* Glossina palpalis.

Host.	No. of hours exposed	No. of bites inflicted	No. of bites per hour.
Varanus	24	60	2·50
Pig	32¼	1	·03
Goat	76	0	·00
Man, African	38	1	·03
,, European ..	202	5	·02

Infestation by fly at the point where the experiment was made was :—Male density 6·0 ; female percentage 15·5.

The strong preference displayed by fly for *Varanus* over the other hosts was confirmed in subsequent experiments. The results with pig proved untrustworthy. It was later discovered (p. 381) that this animal is sometimes, at least, a favoured host.

2. *Comparison between Goat,* Varanus *and Crocodile.*

Two goats, one *Varanus* and one crocodile were used in a short experiment on Kimmi Island on the 27th January 1914. The crocodile was young and active, and between 3 and 4 feet in length. The *Varanus* was slightly larger. All animals were exposed as equally as possible. The crocodile first, and soon after the *Varanus,* became intractable, apparently because of the swarms of flies which assailed them, and the experiment had to be discontinued.

The infestation of this island at this time was :—Male density 24·3 ; female percentage 57·5.

TABLE XXIII.

The Relative Attractiveness of Varanus, *Crocodile and Goat to* Glossina palpalis.

Host.	No. of hours exposed.	No. of bites inflicted.	No. of bites per hour.
Varanus	2	98	49·0
Crocodile	1¾	40	22·8
Goat	4	3	·7

The comparison between *Varanus* and goat is believed to be a fair one. That between *Varanus* and Crocodile is not so fair, because of the small size and greater activity of the crocodile. Both are favoured hosts, and about equally so.

3. *Comparison between Ox, Sheep and* Varanus.

This experiment was conducted in April 1915 on the Peninsula of Nubiru, on the mainland. Two native sheep, both full-grown, were used, and three young bulls about half-grown. One of these was an apparently pure-blooded Ankole (*Bos aegypticus*) ; the second was of a strongly marked zebu or Indian type, with fully developed hump and other characteristics ; the third had the outward appearance of some nondescript European breed, and was probably a half-breed. Special care was used to expose the various animals as equally as possible. The results are summarised in Table XXIV.

TABLE XXIV.

The Relative Attractiveness of Varanus, *Sheep and Ox to* Glossina palpalis.

Host.	No. of hours exposed	No. of bites inflicted.	No. of bites per hour.
Varanus	4	29	7·1
Ankole Bull.. ..	11	32	2·9
Indian ,, ...	11	1	·1
Half-breed ,,.. ..	11	20	1·7
Sheep No. 1	11	1	·1
,, No. 2	11	0	·0

Infestation by fly in this locality was, at this time :—Male density 5·3 ; female percentage 41·2.

There were two extraordinary features of this experiment, one of which is brought out in the table above : the immunity of the Indian bull to attack as compared with the Ankole and half-breed. This was entirely due to his very excitable temperament. He was intractable, and perhaps a bit dangerous, and became almost as excited under attack by *Glossina* as the sheep, which were even more intolerant of fly than the goats used in previous experiments. The Ankole, on the other extreme, was absolutely tractable and docile, and refused to become annoyed at the attack of either *Glossina* or *Stomoxys*, and the half-breed was not much different. Both these animals were covered with ticks, but the Indian would not permit even these pests, and by remarkable contortions succeeded in freeing himself of them on nearly every part of his body.

The second notable feature of the experiment was the behaviour of fly toward the bulls at different hours of the day. The experiment extended over three days. Each day the morning was dull and rainy and each day the animals were taken to the shore as soon as the clouds broke and while the vegetation was still wet. As will be seen by Table XXV the bulls were fed upon much more frequently during the first hours following the clearing, but the *Varanus* was somewhat more freely attacked later on.

TABLE XXV.

Behaviour of Glossina *towards Domestic Ox as affected by Presence of* Tabanus.

Animals.	Bites per hour inflicted during first hours following clearing of weather; *Tabanus* not active	Bites per hour inflicted during later hours: *Tabanus* active.
Ankole Bull	7·3	1·1
Indian ,, ...	·3	·0
Half breed ,, ...	5·0	·7
Varanus	5·0	7·4

The fact that the number of flies feeding on *Varanus* increased after the firs hour, instead of falling off sharply, proved conclusively that the flies were no less active or less willing to feed, and the explanation for the sharp decline in number of bites inflicted on the bulls is unquestionably due to the fact that an hour or so after the clouds broke and when the vegetation was quite dry a large species of *Tabanus* appeared and caused the animals much annoyance. Not even the phlegmatic Ankole would permit these great flies to approach it; the *Glossina* were incidently included in the interdiction, and were effectually prevented from attacking if there was any *Tabanus* about. But no *Tabanus* or any other flies than *Glossina* attacked the *Varanus.*

These experiments were inconclusive in so far as proving the relative status of the domestic ox as a host of *Glossina palpalis;* but they conclusively showed that where such animals are concerned freedom of attack by *Glossina* is to a very large extent determined by the temperament of the individual, and also by extraneous circumstances and conditions of time and place.

The experiments were continued over several days, more in an effort to find some locality where there was tsetse but no *Tabanus*, and also in an effort to induce a "following swarm" to collect on either an ox or *Varanus*, but without result. The cattle found the *Tabanus* so annoying that it was necessary to constrain them to remain near the Lake shore at hours when these flies were active, and they were generally distributed at all points along this reach of shore. The *Varanus*, also proved intractable, and would not remain quiet in restraint. On this account it is believed, the "following swarm" (*vide* Sect. IV) refused to collect.

4. *Comparison between* Varanus *and Man.*

On 31st October 1913 a large *Varanus* was tethered at a point on the shore of Bulago Island infested by *Glossina*. The morning was cool, and few flies were active until about 11 o'clock, when the weather cleared. It was then noted that the observer appeared rather more attractive to them than the *Varanus*.

From noon until 1.30 the animal was left alone, and on returning to it, more than 30 (perhaps more than 50) flies were resting on or near it, and many more were close at hand. Many were feeding, and about 100 were observed to engorge in the course of the afternoon.

No fly bit the observer during this period, and it was estimated that 30 flies came to the reptile to 1 that would come to him—in sharp contrast to the conditions in the morning.

This was a true "following swarm," and the only one that could ever be induced to gather on an animal in captivity or under constraint. The failure of all other experiments in this respect is believed, certainly, to be due to the uneasiness of the animal, and it was long afterwards recalled that the animal in this particular experiment had been quite severely wounded, and was disinclined to activity.

VI (*d*). Approach and Observation of Animals in a Natural Environment to determine Hosts and Host Preferences of *Glossina palpalis*.*

Varanus.

Varanus were approached on a fair number of occasions, and ample confirmation was secured of their attractiveness to tsetse as a host.

Crocodile.

Crocodile was never actually approached, for there are few animals more quick to take alarm at the sound of an intruder, and at the first alarm a crocodile—unlike many other animals—is sure to make off. But on several occasions when they have been seen to slip quietly into the water, the vegetation near the spot where they were resting has been found covered with engorged flies; on one occasion in such numbers that the small bushes nearest at hand seemed thick with red berries.

Si utunga.

Attempts to approach situtunga were singularly successful. Many of the animals on the islands had never seen man, and though the scent of him would stampede them instantly, they were not, as a rule, at all alarmed at the sight of him if he remained motionless. Perhaps a dozen in all were successfully approached.

Notes on behaviour of fly toward this host have already been presented. The behaviour of the host toward fly was rarely positive. They are phlegmatic, and very bovine in their actions, only occasionally showing signs of annoyance by a movement of the head, if flies are very persistent. An exception was a half-grown male, accompanying several adults, which displayed almost continual annoyance, with *Stomoxys* no less than with *Glossina*.

* See also notes on "following swarm," Sect. IV.

No large Tabanids or other large biting flies, apart from *Glossina* and *Stomoxys*, were ever seen on situtunga on the islands.

Tortoise.

Tortoise have twice been encountered on land in infested territory, and on each occasion were accompanied by so many flies as to constitute a " following swarm." The flies were seen to feed on both occasions, and in one instance the animal was very plainly annoyed, frequently brushing the flies from its head with its foot. The flies fed principally on the orbits, and the extent to which the subject had suffered from their attack was witnessed by a whitish ring surrounding each eye composed of the dried serum which is exuded in droplets by the flies while feeding.

Monkeys.

Troops of the *Cercopithecus* monkey common to the region have twice been approached closely enough to observe the movements of flies in their vicinity. The most successful attempt was on Bugalla (Sesse) Island in January 1915. A considerable troop was deployed on the beach at a point where infestation was heavy. Flies could be seen resting on rocks around which the monkeys were foraging (for crabs), but none was seen to approach the animals, nor did the latter show signs of being attacked.

When goats or sheep are driven into infested spots like this, enough flies will approach to keep them on the *qui vive.* There is no doubt that this species of monkey is avoided by fly yet more completely than sheep or goats.

Otter.

The mammalian life on the islands is so lacking in diversity (as compared with the mainland) that otter, next to situtunga, hippopotamus and pig, is the most logical warm-blooded host for tsetse. On three occasions otters were observed on land freely exposed to attack by tsetse and under conditions which would certainly have led to attack upon *Varanus,* but the flies paid no attention to them.

Mongoose.

A large mongoose is common on certain islands—notably Kitobo, where more were seen in a week's time than on all other islands together. It has a habit of basking in the sun, selecting a spot where its ground-colour (much like dead leaves) harmonises completely with its surroundings. By its habits it is freely exposed to attacks of fly, but on several occasions when animals basking in fly-infested spots have been flushed, no fly has been observed.

Domestic Animals.

Cattle were more or less regularly, and goats occasionally, herded on the borders of the fly belt near Entebbe, and fly was occasionally seen on the former. But it was especially noted (after the experiment with cattle at Mbiru described in the preceding sub-section) that the presence of other flies—and others were usually present in very much larger numbers than tsetse—reacted upon the cattle, and their behaviour upon that of *Glossina,* to protect them measurably from attack.

It is one of the most important traits of *Glossina* to be, perhaps, the quickest of all biting flies to detect and evade retaliatory movements on the part of its hosts. There is no large biting fly known to me which does not possess this self-protecting trait; otherwise stated, there is no large biting fly the behaviour of which I have observed that will habitually press its attack upon an aroused and unwilling host regardless of consequences to itself. Recently I have been studying the behaviour of Tabanids of various species toward animals of many kinds in the Washington Zoological Park, and while they are much more persistent than *Glossina,* they clearly "know when they have had enough" and desist from pressing an attack on an unwilling host. It is this same trait that is developed to a conspicuous degree in *Glossina palpalis* which explains the great relative immunity of so many animals, including probably man and monkey. It is doubtful whether it is nearly so strongly developed in *Glossina morsitans.*

Man.

Life in the fly belt affords a perpetual opportunity to observe and study behaviour of fly toward the human host, and the important reactions of the host toward the parasite.

The idea that the European is less freely attacked than the native is apparently baseless, in so far as the original movement of the insect is concerned. The European is more quickly stimulated to retaliatory action—of a purely instinctive and almost uncontrollable sort—than *some* natives, but there is almost or quite as much difference between men as between the Indian and Ankole bulls used in the experiment at Mbiru. Some of my porters or boys would react to the first approach of a tsetse, and these the flies left severely alone, unless there was very great scarcity of other food. Others of my canoe-men were, in contrast, extremely apathetic and phlegmatic, and would not react to anything short of a severe bite,* and such as these were very frequently bitten. Moreover men of phlegmatic temperament would calmly compose themselves to sleep squarely in line with the stream of passing flies along shore, rather than miss recall to the canoe for foraging expeditions, though they might have escaped the fly by going a hundred or two yards inland; and on one occasion something suggestive of the nucleus of a "following swarm" was observed collected upon the sleeping forms of the lazier members of the canoe's crew who had thus exposed themselves to attack.

Next to sleeping men, men engaged in an absorbing occupation are most liable to attack. I estimate to have been bitten 1,500 times in 18 months, and if from this total is subtracted such bites as were inflicted in localities when both male density and female percentage were high, and when the writing of field notes would hardly be undertaken, it is probable that a majority of these bites were inflicted while I was note writing. This was my only absorbing occupation in the fly belt, but the men had many—repairing canoes; manufacture and repair of fishing tackle; cleaning of fibre (for lines and cordage), etc. In such cases the busiest—not, as above, the laziest—men came in for freest attack.

* The bite of *G. palpalis* may be absolutely painless, or it may be almost stinglike in sharpness, or anywhere between.

But most frequently of all, men were bitten while paddling the canoe. If the landing were infested, a number of flies—sometimes from badly infested landings a dozen to twenty—would follow the canoe from shore, and once fairly away from shore would be very loath to leave it. And these flies, seemingly because there was nothing else to do, were remarkably prone to feed *—not at first, but some time after the canoe had left the land. The work of paddling is purely mechanical and rhythmic, and not in the least absorbing except for the steersman, but it is of a sort that cannot well be interrupted to ward off a hovering fly. Consequently the flies would be left undisturbed until one actually bit, when the paddler, if he felt it, would interrupt his work to drive it away. The fly would then pass to another man, and the process might be repeated many times. I have actually seen five men bitten in quick succession by a single fly, and it is not at all easy to follow the movements of a fly in a crowded canoe.

The engorged flies curiously pass forward in the canoe—against the wind of passage—and will cluster on the prow of it. On one occasion, while rounding a densely infested point of land on the Buddu shore and passing too closely in doing so, a swarm of flies assailed the canoe, and in due course a cluster of eight, fully engorged, had formed on the prow.

This rounding of fly-infested points too closely is even more conducive to attack upon man than the departure from fly-infested landings, for if the canoe skirts the shore for any considerable distance it may gather flies in large numbers, and carry them out to sea.

I have not seen flies come to a canoe much, if any, more than a hundred yards out, and not many will come to one over fifty yards out; but at forty or fifty yards a perfect swarm of flies may make a whirlwind descent.

All things considered, the hunter or forager is probably most immune to attack by tsetse of any individual, for his senses are keyed up, and he is wide-awake and conscious of little things without being physically absorbed in any occupation that deters him from warding off a menacing fly. Certainly I have been bitten least frequently while engaged in hunting or in patrolling the shore in fly survey work, always intent on whatever might be taking place in the vicinity.

As noted of cattle, the relative susceptibility or immunity of man and of individual men to attack is very largely a question of temperament, and of conditions and circumstances of time and place—not forgetting to include among these the relative abundance of other food than human blood.

VI (*e*). **Hosts and Host Preferences of** *Glossina* **as determined by Flies found on Animals shot in Fly Belts.**

Crocodile.—Island of Tavu, 13th September 1915.

A crocodile between 9 and 10 feet in length was shot in such manner as completely to paralyse the body but not to stop circulation of blood (these animals will live and move the body vigorously for an hour or more after a brain shot; this

* It is a curious trait of *Glossina morsitans*, and probably also of *palpalis*, to feed in confinement when they would not if unrestrained. Freshly captured, caged flies will usually feed promptly on the body of an animal pressed against the wire screen, when they would most certainly not have fed if uncaught.

one was shot through the neck vertebrae, and did not bleed, as when shot through the brain). "Following swarm" present, estimated at over 100 flies. In course of one hour 18 flies fed. No flies bit or annoyed the observer. Infestation at this point :—Male density 41·0; female percentage 12·2.

Situtunga.—Island of Sesse (Bugalla), 4th October 1914.

A nearly full-grown male was shot in an old plantation on a hill top about 1,000 yards from water at 5.30 p.m. Small "following swarm" of 22 flies present, of which 6 fed. None annoyed observer. Infestations at this point :—Male density 12·0; female percentage 8·0.

Situtunga.—Island of Sesse (Bugalla), 10th October 1914.

Large male shot in old plantations about 500 yards from shore at 11.0 a.m. Day dry, but overcast and conditions unsuitable for fly to be active. Following swarm of from 30 to 40 flies, of which 11 fed. None annoyed observer. Average number following observer through this region (while hunting) between 2 and 3. Infestation at this point (taken after the weather had cleared and flies became more active) :—Male density 15·3; female percentage 23·3.

Situtunga.—Dumo Point, Buddu, 13th June 1915.

Adult female shot about 2.30 p.m. in thick swamp of raphia palms. There were 3 flies following her. Distance 400 to 500 yards from shore, which is marshy and thinly infested. Density at this point (4 boy-hours spent there) nil.

Bush Pig.—Dumo Point, Buddu, 13th June 1915.

Adult male shot about 9 a.m., within 100 yards of spot where situtunga noted above was shot in p.m. No fly.

Bush Pig.—Dumo Point, Buddu, 17th June 1915.

Adult female shot about 5.30 p.m. in guava thicket (mentioned on p. 385) 500 yards from Lake shore. No fly. Infestation at this point :—Male density 8·8; female percentage 21·4.

Altogether 9 bush-pigs were shot in or so near to fly belt that presence of fly on them would have caused no surprise. But none were shot under more favourable conditions than the two noted above. If a situtunga had been shot under the conditions cited in the second case, absence of fly would have caused surprise. In view of the infestation of this particular point, and of no visible cause for it except the frequency and regularity with which it was visited by bush-pigs in search of the falling guavas, considerable surprise was felt that no flies were following this animal. The evidence concerning preference displayed by *Glossina* for this host is conflicting, as in the case of bush-buck.

Bush-buck.—Island of Bunjako, 17th August 1915.

Three nearly full-grown males shot about 12.30 in old plantations about 200 yards from densely infested shore. No fly on animals. Infestation on shore :—Male density 26·0; female percentage 29·1. Infestation at point where animals were shot :—Density 4·5; females 39·2 per cent.

Altogether about 10 or 12 bush-buck were shot under conditions which would have made presence of fly explicable. In only one case was fly found,* but in no case did its absence cause real surprise except in the one cited above. Had these animals been situtunga, absence of fly upon them would have been extraordinarily exceptional. The evidence concerning preference of *Glossina palpalis* for bush-buck is completely conflicting. As in the case of bush-pig, dispersion of fly inland from water indicates bush-buck to be a favoured host, but absence of fly on shot animals indicates the contrary.

Water-buck.—Bugunga Peninsula, 15th August 1915.

Very large male shot about noon, grazing on edge of thicket about 200 yards from shore. Good weather, and boys were catching fly near at hand at the time. No fly on animal. Infestation at this point:—Male density 4·5; female percentage 25·0.

The evidence is negative, in view of the above notes on bush-buck and bush-pig.

Domestic Pig.—Island of Serinya, 15th September 1914.

Large fat female, one of two, shot about 10.30 a.m., 150 yards from shore, behind dense fringe of reeds, in open forest. Day overcast, but clearing. Large following swarm, considering conditions—perhaps 40 flies, of which many fed. Density at this point very low, but tracks of pig followed backwards led to a densely infested reach of shore 500 to 800 yards distant.

A number of pigs were shot on the Island of Bukassa under conditions almost equally favourable, but no following swarm was observed on them. In this case on Serinya the evidence secured in this manner confirms precisely the evidence presented in Sect. V (*c*) leaving no doubt as to the status of domestic pig as a favoured host—at least under certain conditions.

Hippopotamus.—Island of Buninga (Sesse), 26th July 1915.

Adult female shot about 9 a.m. It was apparently sleeping on the shore, and, aroused by approach of canoe, was cut off from the water. Body fell on land, less than 100 yards from the point where shot. Large following swarm (estimated at 125 flies), of which many (estimated at 30 flies) fed. They fed on eyelids, nose, feet and belly, and engorged freely despite the thickness of the skin—evidently on blood in the skin, if this is possible. (It occurred to me afterwards that though gorged or partly gorged flies were seen apparently feeding on the legs and belly, no flies were actually observed engorging except on the eyelids and nose.) Infestation at this point:—Male density 26·0; female percentage 22·0.

This is the one instance in which a hippo was shot (*a*) on land, (*b*) without plunging into water, (*c*) in a fly-infested locality, and (*d*) at an hour when fly was active. The conditions are not easy to meet, but this single case fixes the status of hippo as a favoured host.

* In this case there was but one fly and it is not certain that it was attracted to the antelope.

VI (*f*). **Long-shore Range and Density of Fly as determined by Food Supply on Victoria Nyanza.**

Glossina must, of course, have food, and no other food than the blood of vertebrates is required by flies in confinement. If any other sort is ever taken, evidence or indication that it is required by the flies is entirely lacking.

Evidence is abundant and conclusive that the four most common of the large shore-loving or amphibious animals found in this region are all favoured hosts (crocodile, *Varanus*, situtunga and hippo). Evidence with respect to common game animals of the mainland (bush-buck, bush-pig, water-buck and buffalo) is negative or conflicting, but it would probably be a conservative estimate that the four favoured hosts first mentioned provide 95 per cent. of the food taken by *Glossina palpalis* on the mainland and 98 or 99 per cent. of its food on the islands (excepting the islands of Bunjako and Binga, where bush-buck, etc., occur, and Bukassa, where pig is a factor).

If this is correct, it might be assumed that complete extermination of the four principle hosts would—in the absence of man and domestic animals—cause reduction in density of infestation by 95 to 99 per cent. I think this would undoubtedly follow, if the extermination of the hosts was complete, for there are several reaches of mainland shore in the district of Buddu where absence of all host animals of favoured species from points within range or reach of tsetse from good shelter and good breeding places is specifically correlated with absence of fly. The best case of this sort is illustrated by figure 6 and the explanatory note accompanying it. Another striking case is the Mujuzi colony, which is remarkable in so many ways, and which is illustrated by fig. 5 (p. 388). This colony centres conspicuously at the point (45 in graph) where alone food is plentiful. North of the colony centre (points 46 and 47) there are good breeding grounds and good shelter, but the falling off in density, coupled with the uniquely high female percentage (p. 373), left no doubt that absence of food explained scarcity of fly away from the colony centre.

It is absolutely necessary, however, that adequate protection in the form of both shelter and breeding grounds shall be provided for the insect within reach of food ; otherwise the most abundant supply of the most preferred food is valueless to the species. These conditions occur in many localities, and are described in some detail in discussions on the effect of shelter and breeding grounds on range and density of fly. Small islets, like that south of Dziru or that east of Bubembe (p. 429), may fairly swarm with crocodile and *Varanus*, and, in addition, provide breeding places of the very best, but if devoid of adequate massive shelter they are fly free, or infested only by stragglers from elsewhere.

It is wholly impracticable to attempt a presentation of general data concerning environmental conditions at the many points on the mainland and on the more than 70 islands that were wholly or in part surveyed. (It would require not less that 150 pages of descriptive matter apart from tables and graphs.) The selected cases cited in various connections must suffice, together with the conclusions drawn from a thorough study of original data in the field (November-December 1914), followed by extensive fly surveys (Sesse Islands and the Buddu and Mawakota shores)

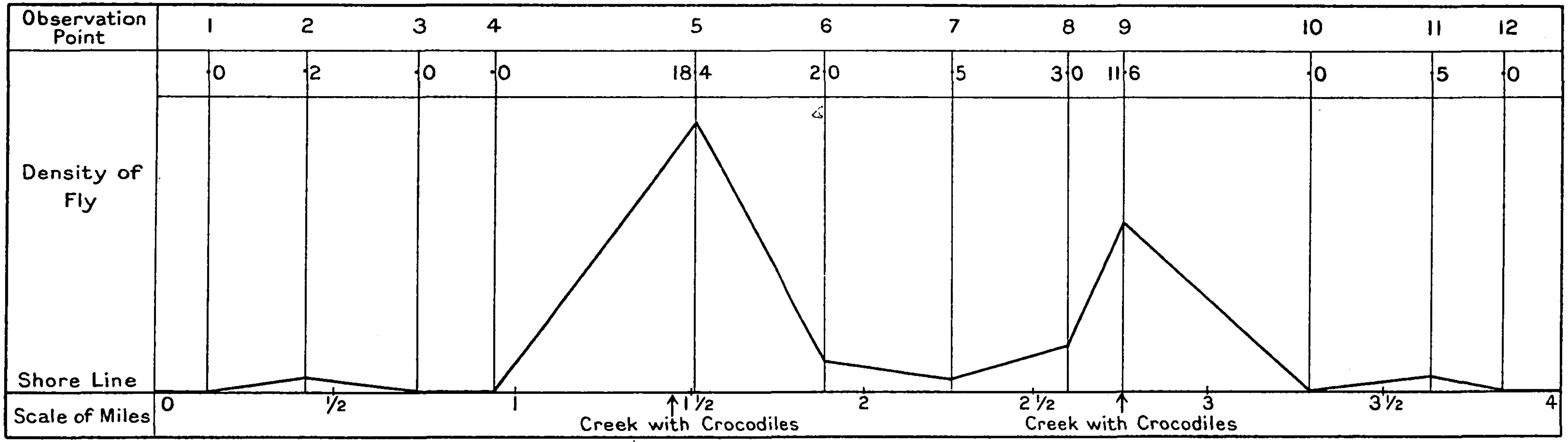

Fig. 6. Fly survey of a reach of shore in the district of Bwendi, Saza of Buddu, showing effect of Crocodile on the range and density of Glossina palpalis.

designed in part to confirm conclusions drawn from co-ordination of data collected in the course of the Island survey, viz. :—

I. If protection (shelter and breeding ground) is more than adequate, range and density of *Glossina palpalis* are controlled by quantity of food of preferred sorts occurring within range or reach of flies from both kinds of protection required (see fig. 6 and note following).

II. Food, even of the most favoured sorts, is valueless to the species unless protection (of both sorts, shelter and breeding grounds) occurs within range or reach of individual flies from it.

III. The distance separating food from protection (as it may be measured by yards) is a factor of the very first importance in determining the prevailing degree of infestation by the species.

VI (*g*). **Effect of Crocodile on Range and Density of Fly along Shore.**

The curve in the accompanying graph (fig. 6) illustrates the variations in local density of *Glossina palpalis* along a reach of four miles of shore which was surveyed in May and June 1915.

The foreshore at these points was an open sandy beach, continuous except at observation points 5 and 9, where it was cut by small creeks. Immediately behind the beach was a belt of open grass-land with a few scattered bushes—not enough to afford shelter for fly. The soil was beach sand, and this open belt or natural clearing was from 40 to 100 yards in width. Behind it was thick bush, jungle and forest, affording excellent shelter for fly; good breeding ground was almost continuous along the border of the woodland from point 1 to point 9.

Food only was lacking. There were tracks of hippo, bush-buck, bush-pig, water-buck and buffalo in the open belt, but the animals were not seen; their spoor was not fresh, and they were obviously only occasional visitors. Crocodiles and the fresh spoor of crocodiles were seen along the water's edge, but they were effectually cut off from shelter by the open belt, and beyond reach of flies.

Only at points 5 and 9, where the creeks cut through the open belt and sand beach, did the crocodiles come into range or reach of flies from shelter. At these points they found harbour in the mouths of the creeks, and basked on their banks within easy reach of the flies from shelter, and here, as the graph clearly shows, two small semi-distinct colonies of fly existed. There could be no doubt that the existence of these colonies was due to the presence of a regular supply of food, represented by the crocodiles, within range or reach of the flies from shelter.

VII. The Breeding Grounds of Glossina Palpalis.

It is a strongly marked characteristic of *Glossina palpalis* to seek specifically protected spots wherein to deposit its larvae, and extraordinary accumulations of puparia and the empty shells of them (from which adults have issued) may be found in especially attractive situations.

To what extent the species is dependent on breeding grounds of sorts easily found, and recognisable as such, was unknown, and it was one of the principle objects of these investigations to secure positive information on this point, and in the hope that it would prove practicable to control the density of the insect by seeking and destroying its specific breeding places.

VII (*a*). **Breeding Grounds on Sand and Gravel Beaches.**

The larva of *Glossina palpalis* is nourished by the female until full-fed and ready to pupate, and is then carried by her and deposited in protected situations known as breeding places. The most attractive breeding grounds are the deposits of clean dry beach sand or gravel that occur more or less frequently along the shore. They must be in or near to the course followed by the streams of moving flies, *i.e.*, very few puparia can be found in situations much off the course of fly traffic—and they must be shaded.

Shade may be afforded by almost anything, provided only that it is not more than two or three feet above the surface of the soil. If much higher the spot will be avoided. Vegetation, both shrubby and herbaceous, rocks, logs, stumps, etc., will provide attractive shelter from the sun. The need of it is imperative, for the larvae never penetrate more than two or three inches below the surface, and the sun striking full on the surface will kill the puparia quickly. Even in the shaded, sand-strewn caves which occur along the shores of certain islands, into which the sun never penetrates, and which are sometimes attractive as breeding places, the flies will only deposit their larvae around the edges, close under the overhanging rock, as though fearful lest the rock farther above the surface of the soil might not provide the continuous shelter required.

In especially attractive spots—if there are not too many of them—large deposits of puparia and puparium shells may frequently be found. The record " catch " which was accurately counted was made in September 1914 on the island of Zinga, beneath an old stump thrown upon the beach by some storm, and overgrown with " morning glory " vines. It required one boy 35 minutes to sift the soil beneath this bit of shelter. In a space hardly more than a yard square he found:

Empty shells	478	Rate per boy hour	814
Healthy puparia	144	,, ,,	247
Total	622	,, ,,	1061

Relatively few accurate counts of puparia and pupal shells were attempted, for unless inordinate pains are taken, the figures mean little or nothing. There may be much or little attractive breeding ground, and if much of it, puparia are difficult to find—if little of it, they are more easy to find. The number of puparia found at different seasons of the year means nothing, for the upspringing or withering of vegetation affects the extent and attractiveness of breeding ground profoundly; and the same is true of the more or less regular fluctuations in level of the lake. The accompanying table (Table XXVI) will indicate the numbers likely to be found by expert fly boys under favourable conditions—as along the " fly beaches " (each locality except that on Tavu Island was a " fly beach ").

For a time it was thought that data on the proportionate numbers of pupae in different stages of their development might be worth collecting, but after a time the idea was discarded. The healthy puparia were opened, and those showing the grey colour of the adult were classed as " late stages," while those showing no colour except on the eyes were classed as " early stages." The data of this character collected are, in part, presented in Table XXVII. They are mainly interesting on account of the much lower percentage of late stages on the island of Kimmi in March 1914 than during the previous January. In this specific case

TABLE XXVI.

Showing Number of Puparia of Glossina palpalis *that may be found per Boy Hour in Attractive Breeding Grounds on Islands in Victoria Nyanza.*

Island.	Date.	Find of Healthy Puparia.		
		Gross.	Per boy per hour.	
			Maxim.	Average.
Tavu	January 1914	586	268	65·1
Wema	February "	1775	196	34·2
Zinga	September "	144	247	—
Damba	February "	797	71	39·3
Yempaita	" "	445	211	49·3
Nsadzi	" "	133	46	16·8

TABLE XXVII.

Showing Variable Proportions of Pupae of Glossina *in Late Stages of Development, possibly indicative of a correspondingly Variable Rate of Reproduction.*

Island.	Date.	Finds of Puparia.		
		Early stages.	Late stages.	Per cent. of later stages.
Wema	February 1914	1228	447	26·7 %
Yempaita	" "	267	157	37·0 %
Damba	" "	349	7	16·9 %
Nsadzi	" "	73	43	36·5 %
Tavu	September 1915	320	79	20·0 %
Karambide	" 1914	6	25	80·6 %
Mugogoya	" "	12	5	29·4 %
Zinga	" "	92	52	36·1 %
Namba	January "	18	6	25·0 %
"	March "	30	12	28·6 %
Kimmi	January "	101	87	46·3 %
"	March "	130	25	16·1 %
Total and Average of total		2626	989	27·3 %
Average by Islands		..	..	33·3 % *

* This is unduly high on account of the find on Karambide, where the high percentage of late stages was due to the breeding grounds being recently abandoned by flies.

especial care was taken to make the count and test a fair one, in connection with the unusual conditions prevailing on the island in January. It was believed at that time that on account of shortage of food the insects were unable to breed at all freely, and that a high proportion of late stages of pupae would confirm this fact. Surely enough, the proportion of late stages was abnormally high—and surely enough, it was abnormally low in March when food had become more plentiful; but whether the data sustain the hypothesis is somewhat doubtful. A more complete account of the experiment is given on page 451.

The proportion of living puparia to empty shells varies extremely, and variations may be due to many causes. The normal proportions would appear to be about 1 to 5 (if there is a " normal "), but there are so many things which might explain variations from it that data are of slight value, except perhaps in special cases. The first citation in the accompanying table is such a special case. The find was made at a spot where *Varanus* had habitually basked, but there were no recent signs of the presence of the animal, and, with its abandonment of its favourite basking spot, the flies ceased to find the spot attractive breeding ground.

Of somewhat greater interest is the percentage of empty shells which have been eaten or destroyed by some predatory creature—ants, or beetle larvae—which extract the contents without completely destroying the shell. The small percentage of eaten shells and the large percentage from which the flies had issued, shown in Table XXIX, is a clear indication of the remarkable degree of protection afforded by good breeding places to the pupae of *Glossina*. The subject is discussed somewhat more fully elsewhere (p. 435).

TABLE XXVIII.

Showing Proportion of Living Puparia of Glossina palpalis *to Empty Shells found on Islands in Victoria Nyanza.*

Island.	Date.	Finds of puparia and empty shells.			
		Puparia.	Empty shells.	Total.	Per cent. of puparia.
Limnaiba	September 1914 ..	3	283	286	1·1 %
Kiuwa	February ,, ..	6	456	462	1·3 %
Kimmi, Pt. 1* . ..	,, ,, ..	17	1077	1094	1·6 %
Damba, Pt. 1.. ..	,, ,, ..	39	1163	1202	3·2 %
Kimmi, Pt. 2* . ..	,, ,, ..	59	1412	1471	4·0 %
Damba, Pt. 2.. ..	,, ,, ..	797	4493	5290	11·1 %
Nsadzi..	,, ,, ..	133	979	1112	11·9 %
Mugogoya	September ,, ..	17	85	102	16·7 %
Zinga	,, ,, ..	144	478	622	23·1 %
Karambide	,, ,, ..	31	79	110	28·2 %
Tavu	,, 1915 ..	207	344	601	34·4 %
Wema	February 1914 ..	1755	3044	4799	36·6 %
Total and Average		3208	13943	17151	18·7 %

* Point 1 on Kimmi Island was in a cave, where the empty shells might be expected to persist indefinitely. Point 2 is the total for several finds elsewhere on the island.

TABLE XXIX.

Showing Degree of Protection against Predatory Destructors provided for pupae of Glossina palpalis *by good Breeding Places.*

Locality. Wema Island, February 1914.	Find of Empty Shells.			
	Fly emerged.	Destroyed by predators.	Total.	Percentage destroyed.
First Beach	46	0	46	0·0 %
Second "	46	5	51	9·8 %
Third "	292	7	299	2·3 %
Fourth "	318	9	327	2·8 %
Fifth "	213	3	216	1·4 %
Sixth "	521	11	532	2·1 %
Eighth "	117	5	122	4·1 %
Total and average ..	1553	40	1593	2·5 %

The need for the secure protection afforded by good breeding places in the case of an insect like *Glossina* is fairly obvious. The adult has taken it upon itself to feed and protect the larva, but the puparia are exposed to all the innumerable parasitic and predatory destructors of Dipterous puparia in general, which are usually common throughout the world. Owing to the fostering care lavished upon the larva, very few young are produced—less than four per month per female—and it is doubtful if the average longevity exceeds four or five months. About the maximum possible rate of increase, therefore, would be 10-fold per generation, as compared with anywhere from several hundred to several thousand fold potential increase for Diptera generally. The species cannot withstand heavy mortality in its pupal stages under such conditions. Secure protection for the puparia is necessary, and the presence of the female in seeking localities for deposition of her larvae where parasites and predatory destructors rarely penetrate is extremely useful to the species. It is doubtful if any better protected places for breeding exist (at all commonly) than those actually selected most freely, in dry, clean deposits of beach sand or gravel. Except for the ants which wander over the surface, such spots are positively avoided by nearly all insects except *Glossina,* and therefore by the predatory and parasitic destructors of insects in general;* and no parasitic or

* It is possibly significant that the most favoured breeding places of the tsetse and of its principal host, the crocodile, are virtually identical. Much the largest deposits of puparia have been found within a few yards of crocodile nests, in the same type of soil, and under the same type of vegetation that serves partially to shade the female crocodile as she "broods" above her egg deposit.

An almost equally striking correlation between breeding places of tsetse in vegetable debris and basking spots of *Varanus,* coupled with the finding of large deposits of puparia in the sunning spots of situtunga, suggests that the specific or characteristic preferences displayed by the flies for these hosts originated in the circumstance that flies feeding on them were most likely to propagate (instead of the converse: that flies propagating on sand beaches or dry vegetable debris would therefore be most likely to feed on animals inhabiting the same localities.)

It is, indeed, most probable that the preference for certain hosts and for certain types of breeding grounds, now developed into specific characteristics, originated coincidentally, and together served to segregate *Glossina palpalis* from its congeners.

predatory entomophagid has attached itself to *Glossina palpalis*, as a "specific enemy," to follow and prey upon it in the protection of its breeding grounds.

VII (*b*). **Breeding Grounds in Vegetable Debris.**

Quite early in these investigations a second and very distinct type of breeding ground was discovered in fine dry vegetable debris—so dry and undecomposed as to be as unattractive to insects in general as the deposits of clean-washed beach sand or gravel which are most favoured breeding places.

These deposits of vegetable debris have been found rather sparingly both under and over rocks and over coarse gravel or pebbles, which preclude soil moisture from rising to dampen them and aid the growth of fungi and other saprophagous organisms. If under rock, they must be in crevices so deep and well protected as not frequently to be wetted by storms. If over rock or pebbles, they are most frequently shaded by fern and composed of fragments of fern fronds and stems—material which does not readily decompose or attract mycetophagous or saprophagous insects or the destructors of insects.

TABLE XXX.

Finds of Shells and Puparia of Glossina palpalis *in Breeding Grounds in Vegetable Debris.*

Island.	Date.	Finds of puparia. (4)			Finds of empty shells.		
		Gross.	Per boy per hour.		Gross.	Per boy per hour.	
			Maximum.	Average.		Maximum.	Average.
Kiuwa .. (1)	Feb. 19, 1914..	3	2	0·5	317	94	57·7
Namba .. (2)	Mar. 17, 1914..	2	4	—	76	155	—
Namba .. (3)	Mar. 17, 1914..	12	6	1·6	173	50	24·7
Nsadzi .. (2)	Feb. 4, 1914..	6	12	—	86	172	—
Karambide . (3)	Aug. 24, 1914..	34	136	—	79	316	—
Mbugwe .. (3)	Sept. 1, 1914..	8	24	—	88	358	—
Mugogoya .. (2)	Sept. 4, 1914..	24	48	—	85	170	—
Limnaiba .. (2)	Sept. 5, 1914..	3	6	—	383	576	—

(1) In very fine, dry debris under rock shelter.
(2) In basking spot of *Varanus* under fern or other low overhanging shelter.
(3) Under fern or other shelter, over pebble or cobble ; in each case a basking ground of *Varanus* was near at hand.
(4) Compare maximum finds with finds from sunny and gravel breeding grounds (Table XXVI, p. 413). The average finds per boy hour in most cases would be not much greater than in the two cases given, for the breeding places are so small, as a rule, that one boy will exhaust them in 15 minutes to half an hour in cases where the breeding ground is specifically associated with a *Varanus* basking ground.

It is precisely in such spots that *Varanus* likes best to sun itself: over a rock or beach of pebbles with its body partly shaded, as by over hanging fern, and partly exposed to the sun.* The same animals return daily to the same places, and n moving about break up and pack down dead stems, twigs, foliage, etc., to form a finely broken, firm-surfaced mass of debris, right at the edge of low overhanging shelter. The result is excellent breeding ground for fly, definitely associated with perhaps its most favoured host, and very many puparia have frequently been found in such spots. Some of the finds made under these conditions are cited in the accompanying Table.

These breeding grounds in vegetable debris are so few and restricted in extent as compared with those in beach sand or gravel that it was for a time believed that they play no part of measurable importance in the bionomics of *Glossina*. Later on, as recounted in Sect. VII (*c*) following, it was concluded that they may play a part of considerable importance locally, or under rather unusual conditions—unusual, that is, for this particular region.

VII (*c*). Observations on Breeding Grounds found at a Distance from the Lake Shore.

Many small, but very few large finds of puparia have been made at points above the old beach line of 1906. The following are the more conspicuous cases.

Bugalla Island, February 1915.

On the bay side of Lutoboka peninsula, Bugalla (Sesse) Island, is a reach of some 2,000 yards of very old beach line, about 100 to 200 yards back from the beach line of 1906. The intervening space is open grass land, the soil being very light and sandy. The forest rises abruptly behind the very old beach line, and continues unbroken to the shore on the lake side of the peninsula. The infestation along the present shore is heavy on the lake side and low on the bay side. The infestation in the forest along the old beach line is heavy, owing to the great numbers of situtunga.

At certain points along this old beach line in the border of the forest, where the vegetation is dense, the antelope have made sunning places for themselves by preventing new growth from springing up in openings left by falling trees. Two such points were found, near together, about 200 yards from the foreshore on the bay side and 400 yards from the shore on the lake side. The infestation was :—

	Male Density.	Female Percentage.
At shore on lake side	24·6	15·8
,, ,, bay side	4·7	58·8
At sunning spots of antelopes	25·0	16·6

In the sunning spots the sandy soil was laid bare by the hoofs of the antelope, and was fine and dry. There were a few bits of it shaded by tangles of dead vines, by fallen logs, or by tufted vegetation of sorts repugnant to the animals, and puparia were found in large numbers. Exact counts were not made, but it was noted that the breeding places were as attractive and as safe as any along the shore, and that the deposits of puparia were larger than could be found at any point along the shore.

* It is perhaps worth noting that both crocodile and *Varanus* like best to bask, not in the full sun, but with a part of the body shaded. The reason was learned through use of tethered *Varanus* in feeding experiments. It was found that an hour or two of exposure to the full effects of the sun would kill the cold-blooded reptile—more quickly by far than similar exposure would kill a warm-blooded animal. *Varanus* at least (and probably crocodile) is more susceptible to "sun-stroke" than man.

The conclusion was reached that under such conditions, with good food in abundance, good shelter and good breeding ground, the fly would exist and thrive at any distance from the water. But it is a very rare combination at points beyond the old beach line of 1906. Usually, when the soil is light and sandy back from the water, it will not sustain vegetation sufficiently dense to serve for shelter, or for protection of any great number of antelope. Had leopards been present on this island the antelope could not have found protection from them in an environment of this sort.

It was furthermore proved by experiment that except at points where the blanket of vegetable mould that covered the sand on the old beach line had been ground under the feet of the antelope and thoroughly dried by the sun, predatory destructors of the puparia were present in exterminative numbers (see p. 443). The breeding places were made by the antelope, which thus came to provide not only food but protection to its parasites.

Bugalla Island, December 1914 *and February* 1915.

In December 1914 a remarkably heavy infestation was found on the very summit of a high hill near the centre of the southernmost peninsula on Bugalla Island. The catch of fly made at this point indicated a male density of 23·0 and female percentage of 2·5—but the record was discarded because the boys flushed a herd of situtunga and caught the " following swarm." Probably a density of 12·0 would be nearer the facts.

The presence of inland breeding grounds was suggested by the circumstance, and by the further fact that infestation was heavier on the summit of the hill than on its slopes. They were sought for at the time, and a special trip was made to the locality in the February following to seek for them again, but without result.

This was the only inland point found on Bugalla Island, except the one above noted, where density of infestation away from the water suggested the presence of breeding places of sufficient extent to permit the fly to exist independently of breeding grounds along shore.

Bujaju Peninsula, July 1915.

The presence of inland breeding grounds was strongly suggested by dispersion of fly, as noted on page 385.

Kitebo Peninsula, August 1915.

Breeding grounds of fair quality were found on a ridge of sand representing an ancient beach line at distances up to 1,100 yards from the water. The conditions (see p. 386) suggested that the infestation at these points was mainly an extension of a riparian colony of fly inland.

Damba Island, October 1915.

Breeding grounds were found on a very old beach line at probably 300 yards from water, in a sunning spot of situtunga, much as noted on Bugalla Island. The infestation appeared to be an extension inland of infestation along shore. Six days were spent in exploration of Damba in search of inland colonies. Infestation inland is general, and at points quite heavy, but at no point could evidence be found indicative of any real centre of infestation with the possible exception of this one.

Mbugwe Island, March 1915.

The one case in which what appeared certainly to be an independent inland colony, and the only case of a colony independent of breeding grounds in sand or gravel except those on tiny islets, is described in Sect. V (*d*). This is a unique and important observation.

VII (*d*). **The "Fly Beaches."**

The very notable attractiveness of shaded deposits of beach sand or gravel to the females of *Glossina palpalis*, coupled with the need of the species for protection during the pupal stages and the high degree of protection provided by the most attractive breeding places, suggested, naturally enough, that these deposits of sand or gravel are requisite to the life of the species, and that a careful survey of the region would reveal a close correlation between extent of breeding ground of this particular character and prevailing local density of the fly.

Attention was first directed toward the "fly beaches," of which there are many on island and mainland shores. They are merely open beaches of anything from fine white sand to coarse brown gravel or small pebbles mingled with more or less sand; sometimes 600 to 1,000 yards or more in length, but usually less, and backed up, first by low, bushy, semi-open shelter and secondly, by more massive shelter such as may be provided by vine-clad cliffs, but which is nearly always provided by forest.

When, as is usually the case, food is plentiful, this combination undoubtedly provides the most favourable conditions of life for tsetse that occur in this region. The combination of light backed by massive shelter is the most attractive of any to the relatively idle male flies, and the combination of light shelter and masses of beach sand or gravel affords the type of breeding ground most attractive to female flies.

In consequence the maximum degree of density (measured always by density of male flies—since activity of females is so variable a quantity) anywhere encountered in the course of these investigations, was along such a beach (Zinga Island—Table XXXI).

But though the fly beaches afford the very best condition of life for *Glossina palpalis*, other combinations are nearly as good. This is brought out by the table accompanying (Table XXXI) in which are compared :—

I. Maximum degree of infestation (male density) encountered during fly survey of islands in January and February 1914 along fly beaches, with maximum infestation encountered elsewhere during same period.

II. Maximum degree of infestation encountered at any time during course of investigations along fly beaches, with maximum infestation encountered at any other points.

These data indicate the absolute maximum of density encountered in the course of the investigations. The average density for the entire region was calculated on the basis of data from the first 300 observation points to be very close to 12·5.

The density at fly beaches is seen to average something over 20·0 points higher than at the most densely infested points other than fly beaches. At the same time infestation elsewhere is often very heavy.

Table XXXI.

Comparison between Maximum Infestations by Glossina palpalis *at Points on Fly Beaches and at other Points on Victoria Nyanza.*

		Locality.	Date.	Infestation by Glossina. Catch.	Male Density.	Female Percentage.
Fly Beaches.	II	Zinga Island	22nd Sept. 1914 ..	206	158·0	23·3 %
		Pt. No. 80, Buddu ..	3rd July, 1915 ..	288	89·5	37·9 %
	I	Wema Island	25th Feb., 1914 ..	203	67 0	34·0 %
		Yempaita Island	24th Feb., 1914 ..	377	59·6	32·2 %
		Damba Island	12th Feb., 1914 ..	269	55·8	6·7 %
		Nsadzi Island	3rd Feb., 1914 ..	391	36·4	16·1 %
Other Points.	II	Mujuzi Colony	24th June, 1915 ..	358	98·0	45·3 %
		Lutoboka Bay	11th Sept., 1914 ..	107	60·7	15·0 %
	I	Tavu Island	15th Jan., 1914 ..	473	62·5	10·4 %
		Bulago Island	22nd Jan., 1914 ..	271	43·4	19·9 %
		Kimmi Island	29th Jan., 1914 ..	366	38 0	53·3 %
		Kiuwa Island	18th Feb., 1914 ..	245	22·2	18·4 %
		Total and averages for fly beaches .		1734	77·7	25·1 %
		Total and averages for other points ..		1820	54·1	27·1 %

VII (*e*). **Breeding Grounds on Old Beach Line.**

In every case cited in Table XXXI of heavy infestation elsewhere than along fly beaches the breeding grounds were found to be in sand or gravel deposits two or three feet above the level of the lake at that time and anywhere from 10 to 100 yards back from the existing shore line. It was quickly obvious that the lake level had fallen recently, and that the character of the shore had frequently undergone radical change in consequence.

What had been a narrow sandy beach open to the lake and overhung by large trees (a fly beach, in other words) had been left high and dry, and was separated from a reed-grown, marshy foreshore by a more or less marshy and open belt, usually grass-grown and closely cropped by grazing hippo. From the water there would be no indication of any open space, or of any sand beach, nor of anything but a bed of reeds and forest to the back of it.

At other points where low flat rocks overgrown with tangled vegetation marked the existing shore line, considerable deposits of beach sand or gravel would be found a little way inland, washed up by the waves upon the shelving rocks, left behind by the receding waters, and hidden by bushy growth.

At yet other points these conditions were reversed, and what had been a rock-bound shore had become a sand or gravel beach backed by a line of rocks hidden by vegetation.

In one case what had been two small islands lying off the shore of a larger one had been united by a low isthmus, and were connected with the larger island by an almost continuous line of "merinde" or ambatch trees growing in the shallowed water.

Many other radical changes in the character of the shore line were noted, and it soon became evident that although the fly was to be found in maximum density along the open fly beaches, the great mass or body of fly bred in the deposits of sand and gravel marking the old beach line, usually hidden from sight.

Moreover in not a few cases it appeared certain that with the recession of the lake conditions of life formerly intolerable for tsetse had become favourable to it in many localities, and that in other localities the effect had been the opposite.

The question of lake level, and of fluctuations of it, was thus injected into the general subject of tsetse bionomics as one of its more important phases. Data were sought, and it was discovered that the old beach line marked the high lake-level of 1906; that the existing low level was likely to be only temporary; and that at any time the waters might rise to the old level.

In consequence great changes and fluctuations in density of tsetse might be expected to occur without other warning than rise or fall of the water. Eventually, in comparing conditions on a certain reach of shore as they existed in 1915, with conditions as they had been specifically described in old reports of the officers employed on Sleeping Sickness Extended Investigations in 1906, it was found that changes in the degree of infestation had been of the most extreme character. The Mujuzi colony, for the most striking example, already mentioned several times, and last cited in Table XXXI just preceding, was non-existent in 1906.

A more detailed account of the changes wrought in specific cases is presented in Sect. XI.

In certain respects no factor in the bionomics of *Glossina palpalis* in this region is more important than this of the fluctuations in lake level, as the breeding places of the insect are affected. The rising waters uproot vegetation, clear the shore, and wash clean the beaches. Falling waters leave ideal conditions of life for tsetse where formerly they were hard or intolerable. Then the rapidly growing, tropical vegetation closes in on the breeding places, gradually shutting them off from the flies, until rising waters shall again open them to occupation.

VII (*f*). **Correlation between Extent and Character of Breeding Grounds and Degree of Infestation of small Islets by** *Glossina palpalis.*

A fly survey of small islets of less than one square mile in Victoria Nyanza was begun in December 1913 and continued through parts of January, February, August and September following. The object was to ascertain the extent to which the degree of infestation is correlated with amount and character of breeding grounds as represented by deposits of beach sand or gravel along either the old or new beach line. *First and last, some 50 islets were visited. Conditions with respect to extent* and character of breeding grounds were extremely diverse. On some islets no deposits of beach sand or gravel could be found—on others they were numerous and extensive. The islets may be roughly assigned to five categories, accordingly as breeding grounds of this type are "very good," "good," "poor," "very poor" or "none," and the accompanying table (Table XXXII) has been framed to include a fairly representative number from each group.

TABLE XXXII.

Fly Survey of Small Islands in Victoria Nyanza showing Lack of Correlation between Extent of Breeding Grounds and Degree of Infestation by Glossina palpalis.

Island.	Note.	Date.	Size (1).	Breeding Grounds.	Infestation. Male Density.	Infestation. Female Ratio.
Tavu	..(6)	Jan. 1914 ..	B or C	Very Good..	46·6	17·1 %
Kimmi . ..	..(5)	Jan. 1914 ..	A	,, ,, ..	37·2	55·3 %
Lukalu West..	..(2)	Feb. 1914 ..	B	,, ,, ..	9·7	28·5 %
Islet S. of Dziru	..(2)	Mar. 1915 ..	D	,, ,, ..	3·8	26·6 %
Lukalu East ..	..(2)	Feb. 1914 ..	D	,, ,, ..	0·0	—
Kukassu ..	..(2)	Aug. 1914 ..	D	,, ,, ..	0 0	—
Dwavannu ..	..(6)	July 1915 ..	C	Good ..	23·0	9·8 %
Manene. ..	..(6)	Mar. 1915 ..	B	,, . ..	17·7	12·4 %
Dyavadermi ..	..(2)	Mar. 1914 ..	B or C	,, . ..	8·0	21·4 %
Kawari West .	..(2)	Dec. 1913 ..	C or D	,, . ..	7·8	12·5 %
Ziro	..(3)	Feb. 1914 ..	A	,, . ..	5·4	23·7 %
Kirengi. ..	..(3)	Feb. 1914 ..	A	,, . ..	3·8	24·7 %
Kizima . ..	..(2)	Jan. 1914 ..	B or C	,, . ..	2·5	11·0 %
Karambidi ..	..(4)	Aug. 1914 ..	B	Poor. ..	16·7	11·7 %
Namba . ..	...(6)	Jan. 1914 ..	A	,, . ..	9·4	7·9 %
Kakide . ..	..(6)	Sept. 1914 ..	D	,, . ..	8·0	—
Kibibi.. ..	..(6)	Sept. 1914 ..	B	,, : ..	7·8	16·2 %
Dziru	..(6)	Sept. 1914 ..	B	,, . ..	7·5	13·4 %
Kawari East ..	..(6)	Dec. 1913 ..	C or D	,, . ..	4·5	4·7 %
Marida . ..	..(3)	Feb. 1914 ..	B or C	,, . ..	4·1	10 8 %
Mugogoya ..	..(4)	Sept. 1914 ..	B	Very Poor..	7·3	4·4 %
Lugazi . ..	..(4)	Dec. 1913 ..	C or D	,, ,, ..	6·0	15·7 %
Kisigalla ..	..(6)	Feb. 1914 ..	D	,, ,, ..	1·7	—
Limnaiba ..	..(6)	Sept. 1914 ..	B	,, ,, ..	1·6	—
Sanga	..(6)	Feb 1914 ..	D	,, ,, ..	0·2	—
Lula	..(4)	Nov. 1913 ..	D	None ..	14·0	6·0 %
Sari	..(4)	Aug. 1915 ..	C	,, . ..	9·6	9·4 %
Dwanga 'Mto .	..(3)	Feb. 1914 ..	B	,, . ..	0·1	—
Semanya ..	..(6)	Dec. 1913 ..	C or D	,, . ..	Trace*	—
Dwanga 'Mkuru	..(3)	Feb. 1914 ..	A	,, . ..	Trace*	—
Dwasengwe ..	..(3)	Feb. 1914 ..	C	,, . ..	0 0	—
Sentette ..	..(6)	Dec. 1913 ..	C or D	,, . ..	0·0	—
Kadenga ..	..(6)	Aug. 1914 ..	C or D	,, . ..	0·0	—
Kaziru . ..	..(6)	Aug. 1914 ..	C or D	,, . ..	0·0	—

* One fly caught possibly followed canoe to island.

(1). Size of islets : A 125 to 625 acres, roughly estimated.
B 25 ,, 125 ,, ,, ,,
C 5 ,, 25 ,, ,, ,,
D 1 ,, 5 ,, ,, ,,

(2). See Sect. VIII. The factor of shelter is paramount.

(3). See Sect. IX, notes on spiders. The factor of natural enemies enters in.

(4). See Sect. VII (*h*), following. The factor of insularity and dispersion of fly as arbitrarily restricted on small islands enters in.

(5). See Sect. VII (*i*), following. The factor of food supply, coupled with that of insularity and restriction of dispersion, enters.

(6). These islands are : (*a*) well sheltered, (*b*) without undue abundance of natural enemies, (*c*) well provided with food, and (*d*) the factor of insularity appears not to count heavily or at all in its effect on infestation. They appear fairly to represent the effect of breeding grounds in sand and gravel on density of tsetse.

Fig. 7. Fly survey of Bugaba Island.

For explanations see text.

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A certain correlation between extent or character of breeding grounds and degree of infestation is at once apparent, but the lack of it is rather more conspicuous than the presence of it. The scarcity of fly on the island of Lukalu West and the islet south of Dziru, and its complete absence on the very small islets of Lukalu East and Kukassu, notwithstanding the presence of good and extensive breeding places, as well as the lightness of infestation on many of the islets falling in the second group (Kizima, Kirengi, Ziro, etc.), is proof that something else that is requisite to the life of the species is either deficient or lacking altogether.

Yet more significant is the relatively heavy infestation of islands like Karambidi, Mugogoya, or most strikingly, Lula, on which breeding grounds of the sand or gravel type are poor, very poor or lacking altogether.

The food supply was adequate or much more than adequate on virtually all these islets, with the single exception of Kimmi. Both crocodile and *Varanus* were common on nearly all the smallest islets, and particularly so on certain of them that were least densely or not at all infested.

Many other factors were taken into account, but none seemed adequate to explain the facts, and in August 1914 it was resolved to extend the fly survey to include long reaches of shore on the larger islands and mainland on the theory that mere insularity (*i.e.*, excessive insularity of tiny islets of only a few acres in extent) might prove the principle source of confusion. A fairly solid foundation for this theory was subsequently found.

The first extensive reach of shore systematically surveyed was the circumference of the island of Bugaba (fig. 7), a reach of some 16½ miles. The results were most encouraging. A summary follows.

The characters of the foreshore of the lake, and of the soil at points along the shore is indicated in the chart by letters, as follows.

Soils of types which will serve as breeding grounds :—

A. Brown beach gravel and sand.
B. White sand, mixed with coarse gravel or small pebbles.
C. Fine sandy soil, or loose sandy loam a little back from the beach line.
D. Pebbles mixed with a little sand and gravel.
E. Flat rock, with sand or gravel lodged in depressions.
F. Wet sandy beaches, overgrown with grass to water's edge.

Soils and shores of types which do not serve as breeding grounds :—

G. Bold rocky shore, sometimes precipitous.
H. Rocky shore, neither very bold nor very flat.
I. Flat rocky shore (without sand or gravel).
J. Rock and marsh ; or marsh with rocks protruding.
K. Clay banks, with or without marshy foreshore.
L. Marsh, with some floating vegetation (sudd).

Shelter immediately back from the fore-shore :—

M. Forest, or very thick bush.
N. Scattered bush, with open spaces.
O. Thick bush fringe, with grass land behind.
} Sufficient shelter for fly.

P. Thin bush fringe, with grass land behind.
Q. Open grass land to water's edge.
} Insufficient shelter for fly.

It is to be noted that concentration of fly is apt to be greatest at a short distance from the breeding ground.

At point 43 shelter at the breeding ground is insufficient and there is a double-peaked colony, greatest concentration occurring on both sides, about equally.

At point 15, where there is a fine "fly beach" with full southern exposure, the trees grow so luxuriantly at the back of it as completely to shade it during the summer months, when the sun is in the north. At points 16 and 17 the breeding grounds are no better, but the sun strikes the beach and the flies tend to concentrate at the border line between light and shade.

Similar explanations apply at other points.

VII (*g*). Correlation between Density of Infestation by *Glossina palpalis* and Location and Extent of Breeding Grounds in Beach Sand in Regions where Food and Shelter are both more than adequate.

Bugaba was the first of the larger islands selected for exhaustive survey. It lies near the centre of the Bugalla-Bukassa group, and in its general aspects resembles those surrounding it.

Its area was roughly estimated at 4,500 acres, made up of (*a*) forest, rather more than one-third; (*b*) open grassland (formerly pasture), about one-third; (*c*) jungle, occupying sites of abandoned villages and plantations, rather less than one-third.

The forest fills the ravines, covers rocky and unarable slopes and ridges, and forms an almost continuous belt along the shore. The grass land lies at the back of the forest belt along the shore, and extends up the slopes to the borders of the old plantations. The villages and plantations were located on a plateau that occupied the whole central portion of the island. None were seen on the shore. There were three canoe landings, with broad foot-paths leading to the villages and plantations.

The shore line was estimated at between 16 and 17 miles. It was sheltered by forest for almost the entire distance. The southern and eastern shores, except in the large southern bay, were generally bold and rocky—at points precipitous. Elsewhere the shore was for the most part marshy, or with clay banks, but with rock at many points. In the aggregate there was between 2 and 2½ miles of sandy or gravelly shore which might be accounted as potential breeding ground. This was broken into numerous short reaches of from 20 to 100 yards in length, distributed irregularly along the shore line.

Infestation by *Glossina* was limited to a narrow belt along shore. At no point could flies be detected more than 400 yards inland, and at only one point could any be found more than 200 yards inland.

The longshore infestation was light. The maximum male density at any of the 48 observations points was 26·0. The average for all points was 6·7—far below the average for the lake region as a whole of approximately 12·5.

Food was plentiful. Crocodiles, *Varanus* and hippo were all common; situtunga had newly immigrated from Sesse (Bugalla) Island, and a few tracks were seen at only one point. The female percentage was very low: 7·9 for the total catch on the island.

The coincidence of infestation with the location and character of the sandy or gravelly reaches that offered potential breeding ground was gratifyingly precise. At or adjacent to every point on the shore where sandy or gravelly soil was exposed to the surface (*i.e.*, not concealed beneath grass or leaf-mould) and properly shaded, the local density of fly exceeded the average. At no point not at or adjacent to potential breeding ground was the average exceeded. At points closely adjacent to breeding ground the shore was invariably infested, whatsoever its character—whether flat or bold, rocky or marshy or clay bank. At no point exceeding 1¼ miles distance from breeding ground did the density exceed 1·0. At various points no flies were caught in from 2 to 5 boy-hours passed there. Absence or scarcity of fly away from breeding ground was, like presence of it at points adjacent, in no manner affected by the character of the shore, as long as it was devoid of sand or gravel deposits.

In brief, the evidence, as far as it went, was entirely confirmatory of the theory that on large islands, at least, the fly requires in addition to food and shelter the protection provided for its pupae by sand or gravel deposits and by nothing else.

Finally, it was estimated that the clearing of bush or forest from about 45 acres, or roughly 1 per cent. of the total or 4 per cent. of the arable area of the island, would suffice virtually to exterminate the fly.

The data collected during this bit of survey work are presented in fig. 6 (p. 411).

VII (*h*). **The Factor of Insularity.**

The fly survey of Bugaba Island disclosed the existence of semi-detached colonies of flies, centring at or very near to the relatively few and short reaches of shore that would serve as breeding grounds.

From these colony centres flies dispersed and infested reaches of shore on either side along which it was plain that conditions of life were unfavourable to the existence of the species, except as migrants from the better protected colony centres, or centres of infestation.

It was very plain that the flies actually living in the zone of dispersion and beyond the protected precincts could not perpetuate themselves unless the females returned to the breeding grounds with their young. The chances that they may do this are best nearest the breeding grounds, and decrease as distance from the breeding grounds increases. Unless gifted with a "homing" instinct they are as likely to seek breeding grounds in the wrong as in the right direction. There is nothing whatever to indicate or suggest that they have any such extraordinary prescience.

On the contrary, the dispersion of fly from centres of infestation in protected precincts is shown by the graph of the Bugaba colonies and others, to be not incomparable to the dispersion of water welling from a spring in an arid region. At the colony centre—*i.e.*, within the protected precincts—the fly is perpetually increasing in density, and as perpetually flowing or dispersing outward into unprotected territory, where its numbers are perpetually decreasing; much as water from a desert spring is continually dispersing outwards into the arid territory surrounding, and as continually being lost by evaporation. There is a perfect natural balance between outflow of water and loss through evaporation; an increased outflow causes more humid conditions near the source and extension of the irrigated area, until increased evaporation compensates, and *vice versa.*

It is much the same with fly. An increased amount or degree of protection at the colony centre, or anything else which is conducive to increased rate of reproduction, leads to increased density of infestation at and near the source of it, and to wider dispersion into the unprotected territory surrounding, until increasing losses through dispersion compensate for increased rate of reproduction.

But if the dispersion of water at the desert spring were to be completely restricted to a very much smaller area than it naturally irrigates, it would tend to accumulate, and the " balance " would be destroyed. And so with fly ; if dispersion of it from protected precincts is arbitrarily restricted—as actually occurs on small islets—the " balance " is destroyed, and almost anything may happen. And, indeed, almost everything likely to happen in such circumstances actually occurs on the small islets in Victoria Nyanza. The balance in the case of this species of insect is indubitably stabilised by dispersion of it from protected precincts, where conditions of life are favourable to numerical increase from generation to generation, into a surrounding unprotected " zone of dispersion," wherein conditions of life are unfavourable to numerical increase.

The mechanism of the balance rarely fails to function smoothly, except when dispersion is in some manner arbitrarily restricted. The islands afford the commonest exceptions.

The islets devoid of sand or gravel breeding places, but yet infested by *Glossina*, afford excellent proof of this conception of the " balance " with *Glossina palpalis*, and this conception provides the explanation for the occurrence of fly under these conditions of extreme insularity.

The very best example is Lula islet, which is almost, or quite, the smallest in the lake that is infested. It contains very good, but very small, breeding grounds in vegetable debris. They are so small that they would certainly not serve as colony centres if located on the shore of a large island, with no restriction upon dispersion of fly from them. But on Lula dispersion is arbitrarily restricted to a space of less than 5 acres, and to an extreme distance of, probably, less than 200 yards. The flies cannot get so far from them that they cannot readily return to them, and in whichsoever direction the flies seek breeding places for their young they are quickly led to this particular spot.

If Lula were a promontory on Kome Island, where conditions along shore are much the same, the infestation would be, as on Kome, extremely light or nil—the flies would naturally disperse from so restricted a bit of protected area if they could. But they are confined, as in a great breeding-cage, in a corner of which their young, if deposited there, will find protection ; and they live as flies in a breeding-cage would live, not because the environment is pleasing or attractive, but because it happens to be favourable to existence and because they cannot well escape it.

The same conditions prevail on Karambidi, Mugogoya, Lugazi, Sari and Limnaiba Islands. All these, except Limnaiba, were infested to a higher degree than the extent and character of the breeding grounds seemed to warrant, until this question of insularity and restriction of dispersion from breeding grounds was considered.

On Limnaiba Island there was a very good, but very small, bit of breeding ground found, and a very much less dense infestation than experience on Lula, Mugogoya, etc., would lead one to expect. Search in this breeding ground disclosed such numbers proportionately, of hatched shells to whole puparia (see Table XXVIII, p. 414) as to prove that a more dense infestation had recently existed; and reduction in density was explicable because of the fact that this particular spot also bore evidence of having been recently abandoned as a basking ground by *Varanus*. A similar instance was encountered on Karambidi, where in what plainly had been until very recently the basking spot of *Varanus* had also been a favoured breeding spot of tsetse, which had been very recently abandoned, as proved in this case by the most exceptional proportion of puparia in a late stage of development.

Of most particular interest in this connection are the circumstances surrounding the occurrence of an island colony of tsetse, breeding exclusively in vegetable debris on the very crest of a heavily forested hill. In this case, cited more at length in Sect. V (*d*), isolation was produced by the forest, which is, like open water, an obstruction to dispersion without being an insuperable obstacle to it.

It can safely be predicted that if any long reach of shore which provides good shelter and plenty of food is found with breeding places in vegetable debris at sufficiently frequent intervals, it will be found infested by fly; for then flies dispersing from one would find another. But such conditions had not been found at the close of these investigations.

VIII. The Shelter Required by Glossina Palpalis.

Two points in the bionomics of *Glossina palpalis* are so conspicuous as to be noted by every observer: its riparian habit, and its dependence on the shelter provided by arborescent or rankly-growing herbaceous vegetation. It is rarely found far from open water and never far from sheltering vegetation.

The effect of water upon range and density of the species appears to be indirect and coincidental, as concluded in Sect. IV; that of shelter is certainly not so. The flies absolutely require the kind of protection it affords them, and the species could not exist in the absence of it.

It was not expected that these studies would lead to any new discoveries concerning the specific types of sheltering vegetation that provide necessary protection, but it was taken too much for granted that where the flies were found in largest numbers the shelter would be, at least, adequate. This proved not so; and it was discovered that the shelter most attractive to the active flies, or that serves best to shade breeding grounds and as protection for the puparia, is frequently inadequate as protection for the inactive flies. Two kinds of shelter are requisite, (*a*) light, such as serves at breeding grounds and for the active flies; and (*b*) massive, or forest-like, which is required by the inactive flies.

In no other manner was it possible to explain the distribution of fly on the islands, as disclosed by the island survey. The idea was made a working hypothesis, and subsequent survey work sufficiently confirmed it, as recounted in the following pages.

VIII (*a*). **Correlation between Character of Shelter and Infestation of small Islands by Fly.**

Reference to Table XXXII will show that though on certain small islands, notably Lukalu East and Kukassu, infestation was nil despite the presence of "very good" breeding grounds. Food, also, was especially common on these islets, and the only reason which could be assigned for absence of fly was the total lack of what has been called " massive shelter " of the sort provided by large trees in masses, or very heavy masses of shrubbery; in short, by either true forest, or by a type of vegetation approximating true forest.

If this were the true explanation it would serve also to account for lightness of infestation on various other islands—notably Lukalu West and Kizima, which possess relatively to such islands as Tavu, Kimmi, and nearly all of those of larger size, but little massive shelter.

TABLE XXXIII.

Showing Correlation between Character of Shelter and Infestation of Small Islands by Glossina palpalis.

Island.	Character of breeding ground.	Character of Shelter.		Infestation.	
		Light.	Massive.	Male density.	Female percentage.
Tavu	Very good	Good	Very good	46·6	17·1
Kimmi	Very good	Very good	Very good	24·3	57·5
Manene	Good	Good	Very good	17·7	12·4
Dwavannu	Good	Good	Good	23·0	9·8
Ziro	Good	Good	Good	5·4	23·7
Kerenge	Good	Good	Good	3·8	24·7
Lukalu West	Very good	Very good	Poor	9·7	28·5
Dyavadermi	Good	Good	Poor	8·0	21·4
Kawari West	Good	Good	Poor	7·8	12·5
Kizima	Good	Good	Poor	2·5	11·0
Islet S. of Dziru	Very good	Very good	Very poor	3·8	26 6
Lukalu East	Very good	Very good	None	Nil.	—
Kukassu	Very good	Very good	None	Nil.	—

Opposed to the theory that massive shelter is necessary was the fact that the active flies showed a strong preference for such light shelter as is provided by low massed shrubbery with open spaces between thickets or clumps of it, masses or clumps of rank-growing herbs, vine-covered bushes, or stumps, etc. This is the kind of shelter that provides shade for the most attractive breeding places, and it is indubitably most attractive to the active flies of both sexes.

Opposed to the theory also was the fact that such long, narrow sand-pits as Crocodile Point on Bulago Island, which are devoid of massive shelter and semi-detached from the main body of the island (or mainland), are apt to be densely infested by fly. There is more and better massive shelter, and much better breeding grounds, on the island of Kizima, for example, than on Crocodile Point, Bulago; yet the infestation of Kizima, in January 1914, was only 2·5 as compared with 22·7 at Crocodile Point.

This last objection is met, however, by the facts disclosed in the catching experiment on Crocodile Point cited in Sect. III (*a*), which proved conclusively enough that the fly population was not permanently resident, but was continually moving, and that virtually all flies infesting it at a given time were likely to move away from it in the course of a day or two, to be replaced by others. On Kizima the flies have not this privilege. They must remain on the islet and put up with whatever shelter it affords, or leave it permanently. If Kizima were a peninsula of Bulago, like Crocodile Point, its light shelter and breeding grounds, and the great quantity of food it provides, would certainly attract to it even more flies than infest Crocodile Point; but it must be concluded that its heavy infestations under such hypothetical conditions, like the heavy infestation actually existing on Crocodile Point, would be, as the other certainly is, due to the existence of good massive shelter within range or reach of the flies infesting it.

These same facts concerning the movements of flies along shore, or along other favourite courses, answer also the first objections made above. The active flies are active with some positive object; the females are seeking either food or breeding places; the males are seeking either food or association with the females. Light shelter provides the best shade for breeding places, and food (*Varanus* and crocodile especially) is most frequently encountered associated with it; therefore it is sought by the females and equally by the males during their hours of activity. At other times (during the night, storms and dull weather generally), both sexes remain in seclusion, and it is then that massive shelter is presumptively necessary for their protection.

A large number of data collected during the course of the survey of small islands sustained this as the true explanation for lightness or absence of infestation on a fair number of them. The data are of a sort not easily presented, and Table XXXIII is suggestive without being conclusive. Reliance in drawing conclusions was principally placed in such comparative studies as between infestations at points such as are illustrated in the sketches accompanying (fig. 8).

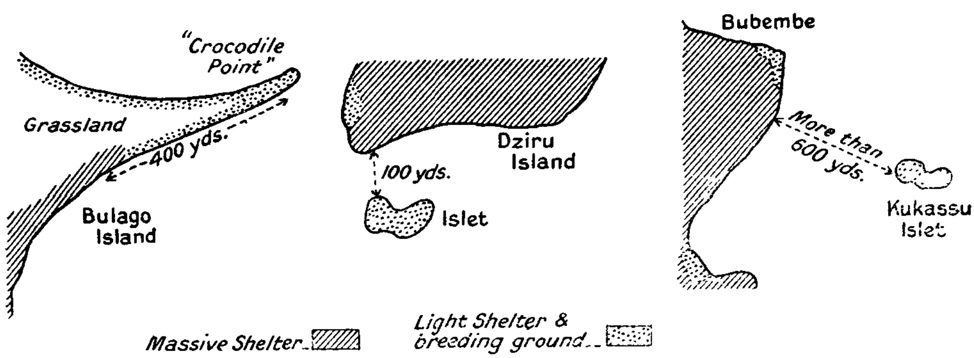

Fig. 8. Illustrating the correlation between character of shelter and infestation of small islands by *Glossina*.

In each of the three cases we have an area of light shelter with good to very good breeding grounds located in certain relations to massive shelter. These three localities are roughly equal in gross area and attractiveness to fly; the two islets being rather superior to the peninsula than otherwise.

The first, at Crocodile Point, lies from 0 to 400 yards from massive shelter on Bulago Island. Infestation was :—

Crocodile Point (Jan. 1914) : male density 22·7 ; female percentage 42·9.

Near massive shelter on south shore of island : male density 20·4 ; female percentage 40·6.

The second area of light shelter and breeding ground was on an islet south of Dziru, and separated from massive shelter by an open channel of about 100 yards in width. This served as a serious obstruction in free movement of fly. Infestation in March 1915 was :—

Islet : male density 3·8 ; female percentage 26·6. Island : male density 5·0 ; female percentage 44·4.

In September 1914 infestation at these same points had been :—

Islet : male density 1·5 ; female percentage 0. Island : male density 6·5 ; female percentage 13·3.

The third area is the islet of Kukassu, which is more than 600 yards off the shore of Bubambe Island, which is the nearest massive shelter. This width of the channel is a complete obstruction to movement of fly. In consequence, infestation, in August 1914, was found to be :—

Kukassu Islet : *nil.*

Bubambe Island (at point opposite) : male density 13·7 ; female percentage 7·8.

These and other data of a similar character provided a weight of evidence that was in the end conclusive ; lightly sheltered areas may provide the best and most attractive hunting, breeding and assembling grounds for *Glossina palpalis,* but unless they lie within easy range or reach of the flies from massive shelter they will not be infested. If there is no obstacle to free movement of flies between such areas and massively sheltered areas, they are apt to be more densely infested than the other. But as distance or obstacles to free movement increase, infestation diminishes, until finally beyond certain limits they cease to be infested.

VIII (*b*). **Correlation between Type of Shelter and Density of Fly as disclosed by Survey of large Islands and Mainland.**

In the beginning it was expected that the survey of small islands and comparisons between them with respect to environmental conditions and density of infestation would be productive of the most valuable data. But it was discovered that insularity, as it affected the normal dispersion of fly (p. 425), was so confusing a factor that the data secured through the survey of long reaches of shore on the mainland and large islands were much more satisfactory.

Especially is this true where the survey reveals, as on Bugaba Island (fig. 7, p. 423), in the Bwendi District (fig. 6, p. 411), at Dumo Point and Mujuzi Creek (fig. 5, p. 388), etc., the existence of well defined, isolated or semi-isolated colonies of fly, each with a sharply defined nucleus, from which flies are continually dispersing to infest a zone surrounding.

The most interesting of all the colonies encountered in the fly survey was certainly that at Mujuzi Creek, of which so much has been written, and which centres at a point where food is provided in a region that is deficient in food. The second in interest is probably that on Lutoboka Bay, illustrated by figure 9, which centres at a point where shelter is adequate in a region that is devoid of good shelter. Study of it in September 1914, and at various subsequent visits, provided evidence deemed absolutely conclusive concerning the need of massive shelter within easy range or reach of *Glossina palpalis*. The colony (fig. 9) is seen to centre at the point where the heavy shelter of a forest belt ceases, and light shelter of a type especially attractive to active flies begins. There are breeding grounds at intervals all the way from point 10 to point 17, but density falls away almost as abruptly in this direction as in the opposite, where light shelter is lacking, and where a positively repulsive belt of sudd (papyrus and saw-grass) fringes the shore.

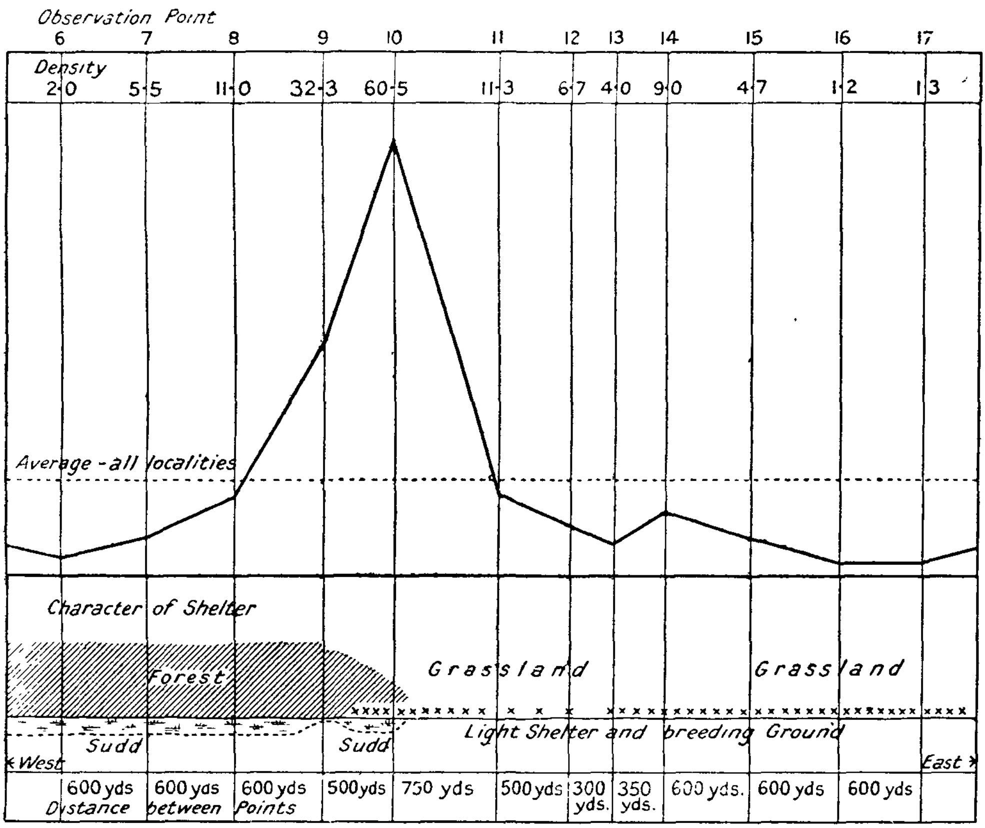

Fig. 9. Diagram showing effect of shelter on range and density of *G. palpalis* in Lutoboka Bay.

Another interesting colony is that shown at points 40 to 46 in figure 7 (p. 423), and also in another connection in figure 3 (p. 371). In this case a short reach of light shelter is flanked on either side by massive shelter, and a double-peaked colony results: *i.e.*, it is either two colonies fused broadly together, or one colony with two nuclei.

An exceedingly interesting reach of shore is one of about five miles along the southern margin of Buganga District in Buddu. Its western extremity is plunged into a great sudd field. Beginning at a point where the sudd gives way and permits landing, there is a reach of 200 yards (estimated) where an almost continuous line of thick shrubbery and other low vegetation grows along a sand embankment which represents the beach line of 1906. Inside this is a short grass, sandy plain, with large herds of water-buck and some zebra. Just outside it are many semi-open spaces of a sort very attractive to fly, with most excellently shaded breeding grounds. Crocodile and hippo are unusually numerous. (Points 1 to 6, inclusive, Table XXXIV.) For the next 2,700 yards the shore becomes very marshy and no attractive shelter could be detected from the water, until at point 8 a narrow ridge of sand outside a belt of light shelter again appeared, continuing to point 9, where for the first time massive shelter was encountered. Beyond this point the shore was diverse and fairly heavily infested.

TABLE XXXIV.

Catches of Fly along Southern Shore of Buganga District, Buddu, showing Effect of Massive Shelter on Density.

Observation point.	Distance beyond preceeding point.	Shelter along shore.		Infestation.		
		Massive.	Light.	Catch.	Male density.	Female percentage.
1 ..	—	None ..	Very good ..	0	—	--
2 ..	900 yds. ..	None ..	Very good ..	4	0·7	0 0
3 ..	600 ,, ..	None ..	Very good ..	1	0·0	100·0
4 ..	800 ,, ..	Very poor ..	Very good ..	9	1·8	0·0
5 ..	900 ,, ..	None ..	Very good ..	0	0·0	—
6 ..	1,000 ,, ..	None ..	Very good ..	1	0·2	0·0
7 .	1,500 ,, ..	Very poor ..	Good ..	8	1·7	37·0
8 ..	1,200 ,, ..	None ..	Good ..	22	2·3*	68·0
9 ..	800 ,, ..	Good ..	Good ..	90	17·0	43·0

* Heavier density represents dispersion from point 9, which was a colony centre.

The point of exceptional interest, however, is No. 4, which was selected as that one where the fringe of light shelter seemed to be the heaviest along this first section of lightly sheltered shore. To all appearances such shelter as was present had sprung up since the high lake-level of 1906, for it was principally growing on an embankment that was the beach line at that time. Moreover, it appeared to be growing heavier and denser in 1915; promising to become, in time, a forest fringe separating the short grass plain from the lake. It had already become so heavy or massive that it would have caused no surprise to have found the shore infested to an average degree. The extreme lightness of the infestation was certainly due to lack of more massive shelter, however, and could not be attributed to any other cause.

But shelter was growing—or seemed to be growing—more massive with each year that passed. It seemed altogether probable that in another year it would become sufficient to protect *Glossina* adequately, and at point 4 the embryo of a future colony appeared actually to exist. Despite the small size of it, it seemed to represent a real independent colony, that would grow, as its protection grew, to become in a few years just such a colony as occurs in the Bukakata district. The conditions of life were almost identically the same in the two localities, except that along the reach of shore in the Bukakata district the vegetation was a few degrees more massive, and afforded that much better protection. The difference cannot be described, and would be difficult to measure, but it represents the line of distinction between shelter that is adequate and shelter that is not adequate to protect the fly.

The main point is that light, low shelter, of the type that is most attractive to the active flies, and that is most certainly to be associated in the mind of the casual observer with the fly, is entirely insufficient to afford the species the protection it requires. Massive or forest-like shelter must be had. It may not exist within several thousand yards of a point where fly occurs, seemingly well satisfied with its environment, but in such cases it will certainly be possible to trace the source of infestation to centres located close to the forest growth.

It may be added that a cliff overgrown with vines and shrubbery has been observed to serve as massive shelter.

Reference back to figure 3 (p. 371) will show again the effect of absence of massive shelter on density.

At points 40, 41, 45 and 46 massive shelter was good but light shelter absent or lacking.

At point 43 light shelter was good but massive shelter lacking.

At points 42 and 44 the light and massive shelter were in juxtaposition, and here were the centres of greatest concentration of fly.

VIII (*c*). **Occurrence of *Glossina palpalis* behind Papyrus or Sudd.**

At many points on islands and mainland narrow belts of floating vegetation (usually papyrus) have formed along sheltered reaches of shore which appear to have been open in 1906—or if not then, very recently. The old beach line of 1906, not infrequently with good breeding grounds, lies behind the sudd belt, which is traversed by passage ways kept open by hippo and crocodile. The crocodiles land and sometimes breed in these places, which retain much of their original character. Fly is commonly found, and in considerable density, in such situations. It would be strange if it were not.

Much of the shore of the lake, especially in the large sheltered bays and channels in the north-western limb of it, is permanently bound by much older fields and banks of sudd. Inside of these the shore line has changed from its original character to resemble the border of a marsh. Sand and gravel beaches, where they existed, have usually been buried beneath humus or are densely overgrown with vegetation.

In July and August 1915 special effort was made to discover if fly were bred under these conditions. The following surveys were made.

Bujaju Peninsula, 30th July and 2nd August 1915.

A great bay (not shown on Whitehouse's Chart) lying west of Bujaju Peninsula is entirely sudd-bound, but with a central channel open. At several points hippo trails traverse the sudd belt. At one point, where the soil is sandy, crocodiles come ashore to breed. The width of the sudd belt is unknown. The distance from the crocodile breeding place to any break in the sudd which would make a canoe landing practicable is not less than 5 miles. The distance across the arm of the peninsula to any point on the eastern shore, or any point where fly has been found inland, is not less than three miles.

What appeared to be a small colony of fly was found. The catch (in 16 boy-hours) was males 5, females 1, giving a density of 13 and female percentage of 16·6.

Bunjako Island, 10th August 1915.

The western shore, separated by sudd-bound channels from the mainland was surveyed for about 5 miles. Situtunga were fairly common at the point, bush-pig common, a few bush-buck, and a very small herd of buffalo; no landing places of amphibious animals, and no trace of fly.

Kitebo Peninsula, 13th August 1915.

Surveyed eastern shore of peninsula, being the western shore of sudd-bound channel separating mainland from Bunjako Island, for distance of 3½ miles north from last break in sudd belt. At the point sandy soil and ancient beach line, semi-open, offered fair breeding places and good shelter. Game not common, no amphibious animals, and no trace of fly beyond the first few hundred yards.

Zinga Island, 20th–22*nd August,* 1915.

Surveyed north-western peninsula (not shown on Whitehouse's Chart) on northern and western shores. It is anciently sudd-bound. Many situtunga were seen and one animal that appeared to be bush-buck; excreta of leopard at one point; no amphibious animals.

Dense infestation at south-western point of the peninsula (where there is no sudd) spread inland for at least 1,000 yards, owing to situtunga. No trace of fly at much more than 1,000 yards from open shore on this portion of island. No sand or gravel found at the back of the old sudd-fields.

Binga Island, 23rd August 1915.

Binga is entirely sudd-bound. The narrowest portion of sudd-belt is about 100 yards in width; except at this one point it is much wider. Bush-buck, bush-pig and buffalo all common; situtunga not common; hippo land frequently where sudd-belt is narrowest.

Fly was found near hippo landings; in 13 boy-hours 11 were caught, making density of ·5, and the female percentage was 45·4 There is a chance that these flies followed the outer border of the sudd-field from the point where it breaks on the stem of Bunjako Island, 3 to 4 miles distant, and that they turned up the hippo trails to Binga. There seemed less probability of this being an independent colony—*i.e.*, a self-perpetuating colony—than in the case of fly caught on the western shore of Bujaju.

Conditions at the back of ancient, permanently anchored fields and belts of sudd 'e somewhat more likely to be favourable to the existence of *Glossina palpalis* ıan conditions at inland points generally, because there is apt to be sandy soil ıfficiently well watered to sustain sheltering vegetation. But it is improbable ıat the necessary combination of food, shelter and breeding places would exist all commonly unless the sudd-belt is so narrow as to permit landing of amphibious ıimals.

It is a safe enough presumption that a sudd-belt not traversed by hippo or crocodile ails is free of fly on its landward side, but narrow belts crossed by hippo or crocodile ails should not be regarded as sufficient protection against fly.

IX. The Inimical Factors in the Bionomics of Glossina palpalis.

The natural enemies and other inimical factors in the bionomics of *Glossina* e numerous and diverse. For this very reason they are peculiarly difficult to identify ıd study. It is much more simple and practical to study the more specific and sily defined protective factors than the more numerous, less specific and less sily defined destructive and otherwise inimical factors against which they afford 'otection.

For example, shade at breeding grounds is protective against the destructive fects of sun, and the clean-washed deposits of sand or gravel which are most favoured breeding places are protection against many different species of parasitic and 'edatory destructors of insects, that are generally distributed and common in most her types of soil than these. If shade at the breeding grounds is destroyed, the ıparia in these are quickly killed by the sun ; and if there are no other breeding ounds left to the fly in that district, it will soon be exterminated, either through ck of protection or through the operation of destructive factors, according to the ›int of view. But though shade is specifically protective against a specific destructive ctor, it is not that factor which operates exterminatively when protection against is destroyed ; it is the parasitic and predatory enemies which become exterminative, ›cause the flies will most certainly not deposit their young in unshaded situations be destroyed by sun. They will seek shaded places, wherein ants, perhaps, or 'ound beetles or beetle larvae, or yet other predatory creatures will be the destructive ;ents, according to the particular spot that they select.

It is impossible in such cases to specify the destructive agents actually responsible r extermination of the species. The breeding grounds are a protection against ›t one or two but against a whole coalition of enemies, any one of which may be :terminative if the flies were to deposit all their larvae in situations exposed to that ırticular one, and all of which are impotent to destroy if the one specific form of 'otection is provided and utilised by the flies.

Moreover it is difficult to see how knowledge of the inimical factors can be made practical application. If we have a knowledge of the protective factors, they n be utilised, for by depriving the insect of its protection very practical utilisation n be made of its destructors. But knowledge of the destructors is valueless unless includes knowledge of the protection which serves the species against them. It is necessary to deprive the fly of protection in any event (before its destructors can be utilised) and knowledge of protective factors in its bionomics must be acquired sooner or later.

The deprivative factors in the bionomics of *Glossina* appear, on the whole, to be more efficacious in restricting its range and density than the destructive. They include all the destructive and otherwise inimical factors in the bionomics of its host species, and, in addition, whatever else may operate to render its food supply less easily accessible or available. But the many deprivative factors are as difficult to identify and define as the destructive, and it is simpler and more practical to study the more specific food factors than to attempt to identify and study the less specific destructors or deprivators of food.

In short, except as a matter of curiosity or technical interest, or as it may assist, sometimes, in confirming conclusions or supplementing evidence bearing on doubtful points, it appears neither necessary nor desirable to devote time and energy to investigation into the identity and nature of the factors inimical to *Glossina palpalis*. If the object for investigation into its bionomics was to cultivate it, as a beneficial species, there would be the same object for studying its enemies that there is for studying it as an enemy of domestic animals or human populations, namely, to find means of protection where protection is lacking. But inasmuch as the object is to destroy and not to cultivate it, and because, obviously, it is protected against all its destructors and other inimical factors in the districts which it infests, it appears much the more logical as well as the simpler and easier course to limit all specialised or intensive studies to the factors responsible for its presence rather than to attempt inclusion of factors manifestly unable to prevent its presence in injurious density. On the face of it, destructive factors are locally impotent and inoperative, and the reason for this must be found before they can be made operative and useful; if it can be learned how the pest is protected against them it may be possible to deprive it of such protection and thus to make practical utilisation of them, but not otherwise.

On these accounts relatively little attention was devoted to the inimical factors in the bionomics of *Glossina palpalis*. A few experiments were made, and these, together with a summary of miscellaneous observations covering a very wide diversity of enemy species, are cited in the following pages.

IX (*a*). **The Hosts of the Fly as Destructive Factors in its Bionomics.**

The bite of the tsetse is frequently painful enough to invite vigorous retaliation on the part of any but the thicker skinned and least sensitive host animals, and an active, sensitive host would thus become a destructive enemy of the first importance if the flies were forced to feed upon it, or were foolish enough to press their attack upon it regardless of consequences.* It is not improbable, however, that the tsetse is

* The very active and very sensitive host is as much an enemy of the flies as any parasite or predatory destructor known. There are many parasites and predators which would destroy the flies if they did not employ self-protective tactics against them; there are several species of host animals which would do the same if the flies were devoid of self-protective instincts. The flies are actually exterminated by neither because of specialised instincts of self-preservation.

quicker to detect danger from this source and more successful in protecting itself against it than any other biting fly. Certainly it is quicker to " dodge " a blow and more difficult to capture bare-handed than any other biting fly known to me, and it is also the quickest to desist from attack upon a dangerously alert and sensitive host.

The most dangerous of its potential hosts are probably monkeys, and it is exceedingly doubtful if it could exist if forced to feed off them alone. Monkeys are not only alert, sensitive and very quick of movement, but are expert catchers of insects.

Sheep and goats are almost equally intolerant, but less dangerous, by far. They strive to evade being bitten rather than to destroy the aggressor.

It was noted of the young bull used in the experiment cited on p. 402 that he strove to destroy his tormentors, striking vigorously with head or foot, in quite sharp contrast to the behaviour of the sheep used in the same experiment.

Man, however, is probably the most potentially destructive host next to monkey. The ordinarily sensitive individual would destroy nearly every fly which he detected in the act of feeding (occasionally the bite is absolutely painless and the fly engorges before being detected), were it not for the extreme quickness of the insect. The chances of a fly's being able to engorge undetected are not at all good, and if deprived of all other than human hosts many would become very hungry before they succeeded in engorging. The very hungry flies take desperate chances, and press their attack so viciously and persistently that they are frequently destroyed. This was characteristic of the flies in the Mujuzi Creek colony, where they pressed their attack so persistently that so many were destroyed as to make it difficult to imagine that the species could exist as a parasite of man alone.*

IX (*b*). **Predatory Destruction of Adult Flies.**

(1). *Spiders.*

One of the conspicuous biotic phenomena along the shores of Victoria Nyanza is the incredible number of spiders that occur locally at points along the mainland shore, or on small islets. There are numerous species, the most conspicuous of which is a gigantic web-spinner identified (by Mr. C. C. Gowdey, Government Entomologist of Uganda) as *Nephele pilipes.* The full-grown individuals of this species habitually stretch their webs from one tree or bush to another across openings in bush or forest, or between the trees and bushes growing not too distantly separated along the lake shore.

There are several other large species which appear like the *Nephele* to be quite independent, and many small species which are not independent, but which live—in proportionately incredible numbers—as guests or inquilines of the larger species—sometimes by robbing their webs of the small insects entangled in them, and sometimes by spinning their finer webs in the coarse meshes of the webs spun by the larger species.

* So alert, quick and sensitive a host as man must be approached by insect parasites with considerable circumspection ; the successful insect parasites of man appear either to approach him while asleep, as in the case of the bed-bug, the floor maggot, most mosquitos, etc., or to be extraordinarily insidious, like the chigger, or to be exceptionally resistent to retaliatory activities like fleas, and some others.

At times the great webs of the *Nephele* are so numerous that in passing through semi-open spaces along shore one must strike them down at every step, and literally hundreds of the gigantic spiders can be seen through openings between the trees, each suspended in the centre of its web and silhouetted against the sky; and not the least remarkable feature of the phenomenon is that one small islet may be thus festooned, and another, a few hundreds or thousands of yards away, may be entirely free. Several of the islets and small islands lying off the shores of Kome (fig. 1) have been found densely infested, but Kome itself has always been entirely free.

These webs are frequently stretched squarely across the courses which would naturally be followed by streams of food-hunting flies, and are inevitably a source of considerable danger. The flies are well aware of it, and remarkably successful in avoiding capture; still many of them become entangled. Of these a fair proportion escape by the strength and vigour of their actions, but a proportion are destroyed.

On the island of Wema, in February 1914, a light infestation by spider and dense infestation by fly afforded opportunity for study, and counts were made of insects as large as or larger than tsetse that were found entangled in the webs, with results as shown in Table XXXV. It should be noted that of the seven tsetse recorded five were found entangled on approaching the webs, and two became entangled while the webs were under examination.

TABLE XXXV.

Insects found entangled in Webs of Nephele pilipes.

Insects.	In webs along fly beach, 27th Feb.	In webs in old plantations, 1st March.	Total.
Odonata	1	2	3
Ephemeridae	4	1	5
Orthoptera (Acridiidae)	4	9	13
Homoptera (Fulgoridae)	0	14	14
Hemiptera	4	4	8
Lepidoptera	9	14	23
Coleoptera	3	6	14
Hymenoptera	8	11	14
Miscellaneous Diptera	5	2	7
Glossina	5	2	7
Total	43	65	108
Percentage Glossina	11·6	3·1 %	6·5 %

The unexpectedly high percentage of *Glossina* amongst the insects of equal or larger size captured by the *Nephele* rendered it extremely probable that where infestation by spider is excessively heavy it must have some effect in reducing local density of tsetse, and it is believed that its effect is fairly measured in the accompanying table (Table XXXVI). The two islands of Ziro and Kerenge were very densely infested by spiders, but otherwise they appeared to be in all respects as favourable to tsetse as the other islands named in the table. Both were accounted "better than Namba" and "as good as Bulago" in the final summing up of impressions gained during the several days spent in the survey of each.

TABLE XXXVI.

Effect of Spider on Density of Glossina palpalis.

Island.	Date.	Character of Environment.				Infestation.	
		Shelter.	Breeding grounds.	Food.	Spider.	Male density.	Female ratio.
Bulago ..	Jan. 1914	Good ..	Good ..	Good ..	None ..	27·5	29·0 %
Nsadzi ..	,, ,,	,, ..	,, ..	,, ..	,, ..	18·4	24·6 %
Kitebo ..	Dec. 1913	,, ..	,, ..	,, ..	,, ..	14·5	33·7 %
Namba ..	Jan. 1914	Very good	Poor ..	Very good	,, ..	9·4	7·9 %
Ziro ..	Feb. 1914	Good ..	Good ..	Good }	Exceeding- }	5·4	23·7 %
Kerenge	,, ,,	,, ..	,, ..	,, }	ly many }	3·8	24·7 %
Average infestation of islands with no spider						17·2	23·3 %
,, ,, ,, ,, ,, many spiders						4·6	24·2 %
Reduced infestation attributed to spider						12·6 =	73·3 %

Numerous other islands were found to be heavily or excessively infested by spiders, but in the case of no others was comparison with spider-free islands so generally fair.

It is possible that if conditions of life otherwise were less favourable than on Ziro and Kerenge, the spiders in comparable density might prove an exterminative destructor. The islands of Dwanga Mkuru, Dwanga Mto and Dwasengwe noted in Table XXXII (p. 422) as very lightly or not at all infested may possibly owe freedom from fly to infestations by spiders, which was fairly heavy in each case, as well as to absence of breeding grounds.

(2). *Dragonflies.*

A dragonfly of a rather small and undetermined species occurs commonly, but irregularly distributed, throughout the islands and riparian belt. There are other species, but this one is conspicuous for its numbers and for a well marked habit of following moving animals and man and feeding off the flies which are attracted to them. Large numbers—in exceptional cases perhaps as many as 40 or 50—of these dragonflies may follow a man along the open shore, and they have been observed to capture tsetse many times.

The species varies greatly in local density from one island or district to another. It was observed most abundantly along the western shore of Bukone Island in September 1914. A fairly complete survey of the island was made and the infestation indicated (male density 8·6; female ratio 23·4 per cent.) was considerably lighter than conditions, apart from the very exceptional number of dragonflies, would have led one to expect. It seemed quite probable that the destructor was responsible for a considerably less heavy infestation than would otherwise have occurred.

There is this difference between spider and dragonfly—that sheltering vegetation is of little or no protective value against spiders, but of much protective value against dragonflies. They will not follow a moving animal into cover, and the flies are not likely to be captured unless they hunt in the open.

Apart from spiders and dragonflies no destructive enemies of tsetse have been observed that appeared to be specifically responsible for appreciable reduction in density of *Glossina palpalis*.

(3). *Bembex.*

A wasp of the genus *Bembex* works somewhat like the dragonfly in following moving animals and picking off flies attracted to them. Its habits have been described by Dr. Carpenter. Though very variable in density it is nowhere excessively common, and at most points was not observed to occur at all. It would stand third in importance of the destructors of adult flies observed at work, but at no point did it appear to produce an appreciable effect on density of fly.

(4). *Miscellaneous Destructors.*

Small lizards are among the most numerous of entomophagous creatures which hunt in the haunts of tsetse, and it has seemed probable that they destroy many flies. They are nearly everywhere common, and vary relatively little in local density.

A fair number of other entomophagids have been observed working in the haunts of tsetse, but none among them has appeared to be sufficiently numerous to be of any consequence as an enemy.

It is to be noted, however, that it is virtually impossible to study the actual or potential destructors of the inactive flies. It is almost impossible to discover the inactive flies without putting them to flight, and nothing is known of the specific dangers that beset them.

IX (*c*). **Parasitic and Predatory Destruction of the Larvae and Puparia.**

(1). *Ants.*

Almost the only insects common at breeding grounds in clean-washed deposits of beach sand and gravel are the ants which run about over the surface. These would destroy the weak larvae of tsetse if the latter did not bury themselves quickly below the surface. The prescience of the female flies guides them to spots where their young are not unduly exposed to this danger.

There are numerous species of ants which will destroy the puparia if encountered, but none of these are known or suspected to burrow beneath the surface of the soil in breeding grounds in search of buried puparia. The " red driver " and some other of the larger ants will carry the puparia away bodily.

In woodland, or where there is a thick blanket of decaying leaves on the surface of the soil, there are species of ants which work under the loosely packed material and which will destroy any Dipterous puparia encountered in it. If flies ever selected such localities as breeding places it is probable that their young would not penetrate deeply enough to escape these wandering ants, but the flies appear never to deposit their young in such places.

It is with ants as with so many other potential destructors, including monkeys and spiders. If flies fed or attempted to feed on monkeys they would be destroyed; if they flew headlong into the webs of spiders their species would probably be exterminated on the spider islands; if they failed to display characteristic prescience in the selection of breeding places, their young would be destroyed by ants, parasites, etc.; but in each case their instincts save them from destruction.

(2). *Hymenopterous Parasites.*

The parasitism of puparia of *Glossina palpalis* in good breeding grounds by Hymenoptera was found to be absolutely negligible. The only instance encountered was on Wema Island, where in a catch of 203 puparia, 3 were found attacked by a small gregarious Chalcidid. A percentage of parasitism at this point of 1·5 was thus indicated. At other points near at hand enough more unbroken puparia were collected and examined to make a total of 1,775, and not another parasitic specimen was found. From other points, first and last, more than 3,000 living puparia were collected and examined, making some 5,000 in all, and no other case of parasitism was encountered.

Occasionally empty shells are found with small round holes such as are left by Hymenopterous parasites in emerging, but except at the one point noted above, examination of such shells has never disclosed the characteristic (and unmistakable) exuviae of such parasites. The selected breeding grounds of the species are practically absolute protection against this class of destructors.

The parasite discovered on Wema bred with the greatest freedom on puparia of *Glossina* in confinement. About one month was required for the generation. It could be an enemy if it would, but its instincts lead it elsewhere than in the breeding places of *Glossina* in search of prey.

(3). *Miscellaneous Predatory Destructors.*

Ground beetles and their larvae of several species, Carabids and Elaterids, are known to be destructive to puparia, and believed to be very destructive to them except in the dry deposits of sand, gravel and fine vegetable debris normally chosen by the female flies. These, or other destructors unknown, frequently destroy appreciable proportions of puparia, varying in different localities. It was thought probable that counts of "eaten" and "hatched" shells found at breeding grounds in sand and gravel would show a much lower proportion of "eaten" than at breeding grounds in vegetable debris. The actual counts, however, showed no great difference and indicated that the degree of protection provided by vegetable debris is almost equal to that provided by beach sand and gravel (Table XXXVII). There is a much greater difference between good and poor breeding places in sand and gravel or in vegetable debris than between sand or gravel as compared with vegetable debris.

The two instances on Mbugwe and Nsadzi Islands where destruction by predators amounted to 27·2 per cent. and 31·2 per cent., respectively, are worthy of special mention. In each case the prescience of the female was deceived by superficial conditions. Both cases were in basking spots of *Varanus.* That on Nsadzi Island was in the very centre of a great tuft of grass that had been killed by overhanging (encroaching) shrubbery. The fine dead leaves of grass had been pressed down by the body of the animal to present a firm smooth surface, quite dry. But underneath, the grass leaves were moist and decaying, and the larvae of tsetse, penetrating the surface and forming puparia in the damp interior were largely destroyed. The case on Mbugwe Island was very different. Here there was a layer of vegetable debris under fern and over pebbles that had been packed so firmly by the body of the *Varanus* that the larvae could only penetrate with difficulty. Many were forced to form puparia only half concealed and of these all were destroyed.

TABLE XXXVII.

Showing Relative Degree of Protection to Puparia of Glossina palpalis *provided by Breeding Grounds in Beach Sands and Gravels and in Vegetable Debris.*

Locality and Date.	Character of breeding ground.	Finds of puparia shells.			Proportion destroyed by predators.
		Hatched.	Eaten.	Total.	
Damba .. Feb. 1914	Coarse sand	1074	89	1163	7·6 %
Kerenge .. Feb. 1914	Sand and gravel ..	152	3	155	2·0 %
Wema .. Feb. 1914	Brown sands and gravels	2974	70	3044	2·3 %
Bugalla .. Sept. 1914	White sand	81	3	84	3·5 %
Zinga .. Sept. 1914	„ „	457	21	478	4·4 %
Damba .. Feb. 1914	„ „	3939	554	4493	12·3 %
Nsadzi .. Feb. 1914	Very fine white sand.	417	86	503	17·1 %
Namba .. Mar. 1914	Vegetable debris ..	76	0	76	—
Mbugwe .. Mar. 1915	„ „ ..	55	0	55	—
Kiuwa .. Feb. 1914	„ „ ..	310	7	317	2·2 %
Karambidi Sept. 1914	„ „ ..	76	3	79	3·9 %
Limnaiba . Sept. 1914	„ „ ..	268	15	283	5·3 %
Mugogoya Sept. 1914	„ „ ..	77	8	85	9·4 %
Mbugwe .. Sept. 1914	„ „ ..	62	24	86	27·2 %
Nsadzi .. Feb. 1914	„ „ ..	55	25	80	31·2 %
Total and average in sand		9044	826	9920	7·0 %*
„ „ „ „ vegetable debris ..		979	82	1061	9·9 %*

* Average by localities.

A yet more striking case of this same sort was observed in the interior of Bugalla Island, where a surface of hard clay was very thinly strewn with gravel. Shelter and surface conditions were very attractive to the flies, and it is probable that many larvae were deposited there, but though an occasional perfectly fresh puparium —formed the same day—was found, no shells or old puparia could be found on any of the several occasions the point was visited. It appeared to be a perfect death-trap.

First and last, a considerable number of experiments were made in the planting of puparia in localities where none could be found, but where it was conceived they might be deposited by females which could find no safe and attractive breeding places. These experiments proved that certain places—notably tufts of a certain species of grass—would afford adequate protection to the puparia if the flies had the prescience to select them. They also proved that in many places which the flies might conceivably select in lieu of better, the puparia would almost certainly be destroyed.

It was concluded rather definitely that the fly would be exterminated by the predatory destructors of puparia if the females were to deposit their young in the massive shelter—*i.e.*, in forest or forest-like shelter—which they require as protection for themselves. It is most especially in such places, where the surface of the soil is covered with dead leaves and leaf-mould, that the puparia are found and destroyed by predators.

IX (*d*). **Inanimate Destructive Factors.**

(1). *Sun.*

There are very few insects which can withstand for long full exposure to sun, and *Glossina* is no exception. Flies have been inadvertently killed through less than half an hour's exposure of the cage in which they were confined. The cage rested on sun-baked earth, however, and if unconfined the flies could probably have lived much longer. But shade, and of a substantial sort, is requisite during the heat of the day, and flies cannot be tempted far from it when the sun is at maximum power.

Sun striking on soil in which puparia are buried no more deeply than the larvae naturally penetrate—rarely more than 1½ or 2 inches—will destroy them quickly.

It not infrequently happens that a week or a fortnight of dry weather will destroy—or at least cause to droop and wither—herbaceous vegetation that previously afforded attractive and adequate shade for breeding grounds, and great numbers of puparia, in the aggregate, are destroyed by drought and sun in this manner. The most curious case was encountered on Tavu Island in September 1915. Very attractive breeding grounds, adequately protected by shrubs of a sort known to the natives as " Kinsembwe," had been exposed by the activities of a defoliating caterpillar (a species of *Acraea*) and quite extraordinary numbers of puparia were destroyed. Game breaking down vegetation at breeding grounds on Bugalla Island produced the same effect on a smaller scale.

All things considered the sun must be regarded as the most destructive—potentially —of any " enemy " of *Glossina palpalis* and the one against which protection is most urgently required.

(2). *Storms.*

Light shelter is sufficient protection against sun, for both pupae and adults. Massive shelter is nevertheless certainly necessary to the species, and the one destructive agency against which it is obviously of much greater protection than light shelter is storms.

It is very difficult to study the effect of storms on adult flies—mainly because they are almost impossible to find except when active. One can only be sure that their hiding places have been discovered by searching at hours when none are active—for they are quick to take flight if disturbed and quickly confused with active flies if there are any about.

It is a strongly marked characteristic of the active flies to seek shelter when a storm is brewing, especially the females, as shown by the accompanying graph (fig. 10), which was secured in the course of an experiment with the streams of moving flies. The catches were made at a point when all the "resident" flies had been caught off, and only those in the passing streams were being caught. About 11 o'clock a storm gathered on the horizon. The temperature fell a few degrees, and a light breeze sprung up. This was all that happened. The sun was not obscured, and the storm did not come within miles of the island (Manene, 17th March 1915), but almost half the females sought shelter, and remained secluded until the cool breeze dropped. Then they quickly became even more active than before.

Certainly the insects would not flee so quickly at first signs of a storm unless they were fearful of it, and next to sun, storms are probably the most dangerous "enemy" of the species.

(3). *Flood.*

The rising waters of lake or stream may destroy many puparia in breeding grounds in sand or gravel deposits, and would destroy many more than is in fact the case were it not that the females avoid depositing their larvae in spots too near the water. Even on the "fly beaches" it is in the old beach line beyond reach of even the heaviest waves that nearly all the large deposits of pupae have been found.

The effect of such a flood tide as that of 1906 upon the puparia must be very destructive, for in May and June of that year there could have been very few good breeding places—relatively—beyond reach of the waves (see p. 457).

In the bed of the Victoria Nile, some miles from its source, excellent and much frequented breeding grounds were found (April 1914) at points where they would almost certainly be destroyed in May or June.

(4). *Fire.*

Bush or grass fires are potent factors in the bionomics of *Glossina morsitans*, but at no point visited on the islands or riparian zone of Victoria Nyanza was fire likely to affect *Glossina palpalis* to an appreciable extent.

IX (*e*). **Secondary Environmental Factors detrimental to** *Glossina.*

Whatever benefit may be derived by humanity from the activities of the two natural enemies of *Glossina palpalis* which produced an appreciable effect on its density—spider and dragonfly—is inseparably associated with whatever it is which permits these entomophagids to multiply to such excessive numbers as is required to produce that effect.

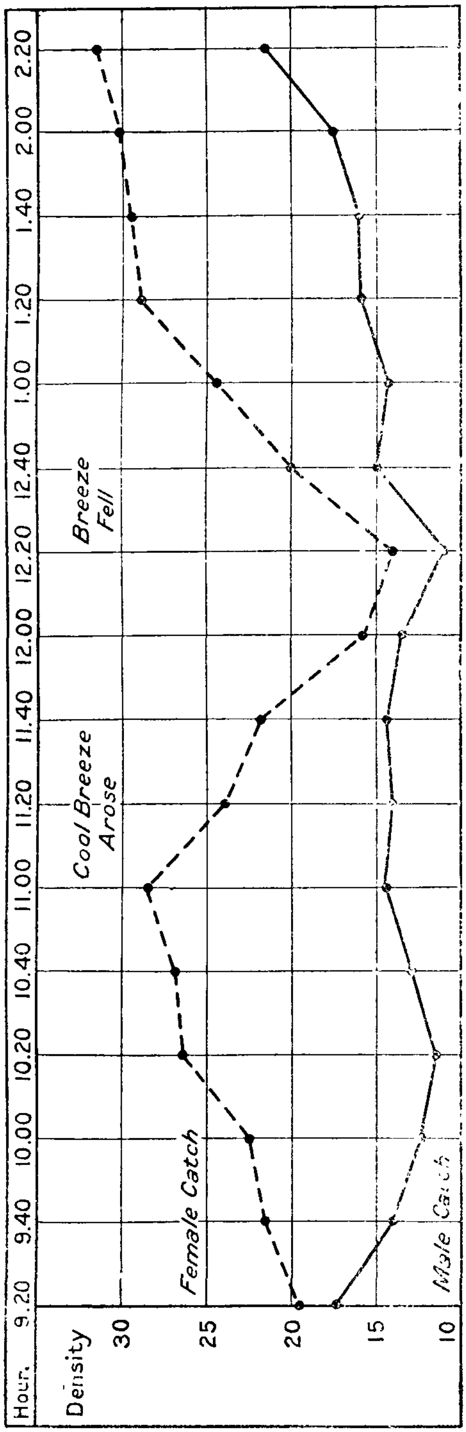

Fig. 10. Diagram showing effect on activities of *Glossina palpalis* of a storm passing at a distance.

Nothing but " insularity " could be attributed as the determining factor in the case of spider. Its great abundance is partly due to the incredible numbers of " lake flies " (*Chironomus*, mainly) which breed in the lake and frequently rise from it in such swarms as to appear like the smoke of a large steamer on the horizon. Swarms of them that must number thousands of millions gather and sweep on shore, where, if there chances to be a generation of newly hatched spiders coming on, they provide an abundance of food at a critical time. Possibly there is some correlation between the incidence of lake fly and of spider, which works out to the disadvantage of *Glossina* in the end.

There is less mystery in the case of the dragonfly. The particular species before mentioned feeds as nymphs in shallow, rush-grown water, more particularly where there is sand and pebbly bottom. The existence of such shallows off shore is detrimental to tsetse on shore.

The *Bembex* breeds in fine, dry sand, of a sort that it can burrow into without its galleries collapsing. It is very irregularly distributed, because this type of soil is not at all common. The type is mildly detrimental to tsetse where it occurs.

Absence of rock, both on shore and in the shallows off shore, is a more potent factor in its inimical effect on tsetse, for *Varanus* is a rock-dweller on land, and its most favoured food is the crabs and molluscs—especially the crabs—which are only found in rocky shallows. There are long reaches of sandy shore south of Dumo village, in Buddu, which are virtually free from fly because of absence of food ; only crocodile occurs, and only at a few points where buck comes down to the water are flies and crocodiles likely to meet.

No trace of *Varanus* was seen along these reaches. Had it occurred (*i.e.*, if there had been food for it, and a rock-bound bottom), its inland wanderings across the natural clearing that bordered the shore would have brought it into contact with shelter and breeding places, and conditions of life would have been excellent for tsetse.

IX (*f*). **Leopard as a Deprivative Enemy of** *Glossina palpalis*.

Through a combination of partly fortuitous circumstances it is possible to measure or estimate, roughly, the effect of the presence and activities of leopards in restricting the range and density of *Glossina palpalis*. It is plainly a more efficacious deprivative enemy than spider is a destructive enemy of the insect. The data follow, item by item.

(1). On the Sesse Islands there are no leopards or other large beasts of prey. Following elimination of the human factor situtunga increased at a rapid rate on every island where it occurred, and spread from the marshes to the hills and abandoned plantations. As a result the range of fly inland increased from a low average of perhaps 300 yards—not counting stragglers—to one that is at least 5 times greater wherever shelter is good and continuous for this distance inland.

(2). On the two sudd-bound islands of Bunjako and Binga leopard occurred, and also situtunga. There was no increase of the latter, nor could evidence be found on Bunjako, which is densely fly-infested along its shore, of more than ordinary extension of infestation inland.

(3). On the island of Bussi, largely sudd-bound, but previous to 1909 separated from the mainland by a canoe track through the sudd, no leopard formerly occurred. The canoe track was choked by sudd, however, and leopards crossed it soon after the eastern shore of the island was depopulated. In October 1914 the island was surveyed for game and inland infestation by fly. Nowhere else were the excreta of leopards discovered in such extraordinary quantity, and examination of them—exact figures were not kept—disclosed unmistakable remains of either situtunga or monkey in nearly every case. No other traces of situtunga were found on the island except, as is usual on the mainland, along the borders of the sudd-fields. There was no inland extension to the infestation by fly, which was fairly dense along the shore.

(4). Zinga Island was sudd-bound like Bussi, and like it, separated from the mainland by a canoe track. It was said by the natives to be entirely free from leopards. Situtunga increased to very large numbers, as on the Sesse Islands, and extended its range inland. The range of fly was also extended inland up to at least 1,000 yards. In exploring the island for inland infestation in August 1915 fresh excreta of leopard were found, and examination of the old canoe track showed that it had become broadly choked with sudd. If the history of the incursion of leopards in Bussi is repeated, the animals should become very numerous by about 1920; situtunga should be driven back into the protection of the sudd-fields, and monkeys, which were excessively numerous in 1915, should be greatly reduced in density.

(5). At no point on the mainland has situtunga increased to much, if at all, beyond its former density, nor has it extended its range beyond easy reach of the animals from the protection of sudd-fields and marshes.

(6). At about three points on the mainland where the local environment affords exceptionally good protection to bush-buck, inland extension of infestation by fly corresponds to that on islands where leopard is absent and situtunga has increased to exceptional density.

There can be no doubt that the range and density of situtunga are controlled by the leopard, which is unable to harm it in the protection afforded by sudd-fields and marshes, but which hunts it assiduously along the border of these protected precincts. There can be little doubt that the range and density of bush-buck are controlled in the same manner; protection in its case being provided by densely tangled thickets, through which it plunges with strange facility, and within which no large animal can approach it without betraying itself.

Wherever leopard is absent and situtunga present in sufficient density, range of fly is extended inland, and situtunga has increased or is increasing (if present at all) everywhere that leopard is absent. There is every reason to assume that bush-buck would do the same, in the absence of leopard and of human hunters.

The correlation is perfect at every point, and it is an entirely reasonable conclusion that in the absence of leopard inland range of fly would on the average be as extensive along well protected portions of the riparian belt as on the islands where situtunga has increased or as at the few points along the mainland shore where the bush-buck has found exceptionally secure protection.

There would be inland extension of infestation to approximately 5 times its present depth at many points, and along extensive reaches of mainland shore, if it were not for the deprivative effect of the activities of leopards. They are certainly a more efficacious natural enemy of the tsetse than spiders, or than any other destructive enemy that has been identified.

IX (*g*). Relations between *Glossina palpalis* and other Biting Flies.

The data secured during the experiments with cattle described in Sect. VI (*c*) (Table XXV) indicated that the presence of other biting flies than *Glossina* might have an effect on host animals that would effectually prevent *Glossina* from feeding upon them. This has since been confirmed in various ways; partly by a series of observations on the behaviour of domestic animals, or of animals in Zoological Gardens, under attack by flies of various species. The Zoological Park at Washington affords particularly good opportunities for such observations, being situated well out from the city in a naturally wooded ravine where *Stomoxys* and *Tabanus* are numerous. Not less than 25 species of ungulates occupy paddocks that are badly infested by these flies, and various others, including several of the familiar game animals of Africa, have runways that are partly exposed.

Variations in degree of tolerance or intolerance to attack were very remarkable, ranging from the absolute intolerance of Barbary sheep, which would seek the seclusion of their hut at the approach of a single *Stomoxys*, to the phlegmatic indifference of red deer, and wapiti, which would permit *Tabanus* to engorge without serious protest. But there was no animal that was not roused to protest and retaliation if flies became too numerous and persistent, and any animal that is thoroughly aroused and excited becomes of little value as a host to any biting fly.

Eland, for example, was passive under attack by *Stomoxys* in moderate numbers, but repeatedly on approach of *Tabanus* the animals would betray annoyance, and move to protect themselves not only against the greater but the lesser pest. A single *Tabanus* would cause all the elands to seek shelter, and effectually deprive several dozen *Stomoxys* of this particular source of food. Bison was more tolerant than eland, but a few *Tabanus* would sometimes set a whole herd in motion. Zebra and wild horse were less tolerant than eland, but would suffer *Stomoxys* to feed in small numbers until *Tabanus* appeared.

None of the larger biting flies observed on these or any other occasions have pressed their attack on an unwilling host regardless of risk to themselves, but none has shown more regard for its own safety or been quicker to desist from attack upon an intolerant host than *Glossina palpalis*. A *Tabanus* has been observed to return to the attack more than 30 times before admitting defeat. A *Glossina*, unless positively famishing, doubtfully returns more than 4 or 5 times at the most—perhaps not more than once or twice. With man they usually desist after the very first repulse. The more persistent pest may, therefore (as shown by the experiment—Table XXV) become a very efficacious deprivative enemy of the less persistent and the effect is felt in two distinctly different ways:—(*a*) the host animal may be induced to leave a locality or district where it is liable to be annoyed, or (*b*) the less persistent and more easily discouraged flies may be induced to leave the locality where a more persistent and annoying species is active.

The dependence of *Glossina palpalis* upon specific forms of protection—breeding grounds and shelter—has been shown in Sects. VII and VIII. Except when provided with both kinds within easy reach (of the flies) from each other the species cannot exist. Where both kinds occur in sufficient proximity the fly can exist if also provided with food, but food, also, must be within easy reach of flies from both kinds of protection.

It is this factor of the actual location of food with respect to protection that counts most heavily in determining the range and density of fly. It is much less a question how much food—how many host animals—exists in a given region or district, or on a given island, than it is one of the quantity of food or number of host animals existing in the adequately protected precincts. It is not necessary that the host animals shall be destroyed in order to injure the fly; but is quite sufficient that they should move a little outside the range or reach of flies from either shelter or breeding places.

Therefore if the animal is induced by *Tabanus*, or any other biting fly, to move a little farther away from the specifically protected precincts, *Glossina* is forced to follow, and in following is exposed to all the risks, and enemies of a destructive nature, that make specific protection a requisite for its existence. The effect of the rival is precisely equivalent to either of the following :—(*a*) reduction in quantity of available food, (*b*) reduction in quantity or degree of protection, or (*c*) increase in number or destructiveness of enemies.

This is if the host is induced to leave the locality. It is the same if retaliatory activities on the part of the host induce the flies to desist from attack and to move on in search of another, more submissive animal. To do this the flies must leave protected precincts and undergo greater risk of being destroyed themselves, or of being unable to find protection for their young.

The activities of *Tabanus* have the direct effect of reducing the quantity of available food in protected precincts, which is the equivalent of either reducing the amount of degree of protection, or increasing the number or destructiveness of enemies.

IX (*h*). **Super-density of** *Glossina palpalis*.

There appears to be nothing to prevent the multiplication of *Glossina palpalis* to any degree of density which the food supply permits in any locality where protection is provided for it, except the continued dispersion of flies outwards from the protected precincts to infest a surrounding zone of unprotected territory. Within the protected precincts the natural increase of the species is greater than the mortality, but gain through natural increase is equal to loss through mortality plus loss through dispersion. Hence density does not increase beyond certain limits, because when the flies become sufficiently numerous to arouse their host animals to the point of retaliation, the immediate effect is to accelerate dispersion, thus reducing density in the protective precincts. Outside these precincts mortality is greater than reproduction, but loss through mortality is equal to gain through natural increase plus gain through immigration.

A delicate " natural balance " is thus created, which remains in a state of great stability as long as nothing interferes with the free dispersion of flies. Super-density (or " outbreak " or " epidemic ") of fly is impossible. It cannot increase so as to cause direct injury to its host species through excessive blood-letting; it cannot even increase so as to cause its host animals excessive annoyance.

But if dispersion is for any reason obstructed or interfered with, the mechanism of the balance between the fly and it host species is thrown out of gear, and its density continues to increase until in their own protection its hosts are forced to abandon their haunts. The fly thus becomes an " enemy " of its hosts in actuality. It has " broken out " or become " epidemic," in the terminology of economic entomology. It has increased to a state of super-density when the flies have become the real deprivative enemies of each other, just as flies of the genus *Tabanus* may become the deprivative enemies of tsetse-flies. One tsetse can be the deprivative or competitive enemy of another as easily as a *Tabanus* can be the enemy of a tsetse.

On a very few occasions only were such conditions found to prevail in the region covered by these investigations. The first instance was on the island of Kimmi, which alone of all the islands visited—some 70 in all—appeared to constitute almost entirely a protected area. There was no opportunity for dispersion from it unless the flies struck out over open water, which they were plainly loath to do, and there was hardly a spot on the island where the flies could fail to find both shelter and breeding grounds within easy reach. There was no apparent reason why density should not increase under such circumstances to the point of super-density, which would either injure the host animals or force them to abandon the district.

Conditions encountered on this island in January 1914 indicated that something of this sort was actually taking place. The infestation was heavy (37·2 according to methods finally accepted for estimating male density) and the female percentage was very high (63·5 in total catch and 55·3 at the lowest estimate). The flies were as ravenous as the sex ratio indicates, and host animals seen during 3½ days spent on the island by Dr. Carpenter and me totalled a single *Varanus* seen by him and a single hippo heard crashing about in a reed thicket by me.

No crocodiles were seen, but there was abundant evidence of their very recent presence in the form of nesting places with hatched egg-shells, and runways through the reed fringe along the fore-shore. There was also plenty of evidence of the recent presence of *Varanus*, the mounds thrown up by which were more numerous on this than on any other island visited, except Manene. It seemed not at all improbable that the fly had actually increased to such super-density as to force even the crocodiles to abandon the island, temporarily, until the density of the pest should be reduced.

This idea was sustained by the failure of the experiment cited in Sect. VI (*c*), Table XXIII (p. 402), in which tethered crocodile and *Varanus* (on this same island at this same time) became so quickly intractable under attack that experiments had to be discontinued.

The idea also suggested the following experiment:—

If, as appeared probable, super-density of fly had caused the host animals to abandon the island temporarily, the sudden deprivation of food would result in a quick fall in the number of young produced.* If such decrease in rate of reproduction had taken place within the period of 3 to 4 weeks required for the pupal stages, the fact would be disclosed by examination of the puparia, and the proportionate numbers of them found in early and late stages of development. At a certain late stage in development the pupa is found within the puparium shell showing traces of adult coloration. Such pupae must have been from larvae deposited at least two weeks before. In freshly formed puparia the pupa is unrecognisable, and it requires at least two weeks for it to form and to acquire colour, except in the eyes, which are coloured almost as soon as it takes recognisable form. A count of late and early stages of puparia collected at various points on Kimmi Island was therefore made, and as a check upon it some 3,000 puparia collected in various other localities were examined and counted to ascertain the normal proportions.

The normal, as indicated by the check, was 27·3 per cent. late stages, but on Kimmi Island the late stages composed 46·3 per cent. of the total found and examined. There should have been—if the normal is correctly calculated—very close to 16 early stage to 6 late stage puparia ; actually there were only 7 early to 6 late, indicating that less than half as many young were being produced at the time the collection was made as were being produced two to three weeks before.

In March the island was revisited, the infestations measured, and a second search made for puparia. Conditions were changed notably. Density was somewhat lower than in January, but food had become more plentiful, female percentage had dropped to a figure not far above the ordinary, and the flies were no longer ravenous or especially troublesome. The examination of puparia disclosed only

TABLE XXXVIII.

Showing Variation in Rate of Reproduction (Number of Young produced) of Glossina palpalis *as reflected by Proportion of Late and Early Stages of Puparia.*

Analysis of finds of puparia.	Kimmi Island. January 1914.	Total and averages from numerous localities (1) (showing normal).	Kimmi Island. March 1914.
No. of puparia found	188	3615	155
No. of early stages	101	2626	130
No. of late stages	87	989	25
Percentage of late stages	46·3 %	27·3 % (2)	16·1 %
Ratio of late to early	1 : 1·16	1 : 2·66 (2)	1 : 5·20
Excess or deficit, early stages	— 56 %	0	+ 95 %

(1) See Sect. VII (*a*), Table XXVII.
(2) This ratio would be a constant if the rate of reproduction of the species (number of young deposited) did not vary.

* The females nourish the young larva until it is full fed and ready to transform into the pupa, equal in size to herself. Normally she must feed (engorge) at least 3, probably 4 and possibly 5 times in order to provide sufficient food for a single larva.

16·1 per cent. of late stages. There should have been 16 early to 6 late stages, whereas there were found approximately 32 early to 6 late, or almost exactly twice more than normal, indicating that the flies were depositing twice as many young as were being deposited two or three weeks before.

The experiments were conducted with sufficient care to eliminate most chances of error, and little doubt is felt that there was actually a falling off in the number of young produced followed by a proportionately heavy increase in numbers. The only question is whether this falling off was due, as assumed, to the temporary abandonment of the island by host animals, and whether this in its turn was due, as assumed, to increase in density of fly. The experiment turned out exactly as it should, in accordance with the working hypothesis. It sustains the hypothesis, though it does not prove it. The point in question is, in fact, one that could only be proved by investigations conducted over a considerable period on an island like Kimmi, with exact observations on the movements of host animals and variations in degree of infestation.

Table XXXIX.

Showing Variation in Infestation of Kimmi Island between January and March 1914.

Observation point.	Infestation in January.			Infestation in March.		
	Catch.	Male density.	Female percentage.	Catch.	Male density.	Female percentage.
S.W. Point	384	23·3	62·9 %	208	19·1	26·8 %
N.W. Point	272	43·3	52·2 %	502	45·6	27·3 %
S.E. Point	506	39·5	53·2 %	351	31·7	27·4 %
Southern Shore	276	42·7	53·0 %	292	31·5	13·7 %
Totals and Averages ..	1438	37·2	53·3 %	1353	32·0	23·7 %

The only other localities visited in the course of these investigations in which the female percentage was in excess of 50 (for the entire island or district) are:—

(1) Bunyama Island (data mislaid*) .. .. ..
(2) Bale Beach and Mujuzi Creek colony .. .. 64·6%
(3) Bukakata South colony .. .. 51·0%
(4) Kaziru District (Buddu) .. .. 50·6%

* Since recovered, but not included here.

In none of these localities did it appear that scarcity of food was due to density of fly. The fly was suffering from want of food, certainly, but merely because there was so little food and this so hard to find. Conditions were as they would become on Kimmi if the host animals abandoned the island permanently, all save two or three *Varanus* or a single crocodile. The point where food chanced to be, at any time, would then be a " colony centre "—exactly like the colony centres in the

Bwendi district (fig. 6, p. 411) or at Mujuzi Creek, and there would be dispersion from them as from the points in the Bwendi district or from the point at the mouth of Mujuzi Creek where crocodiles harbour (p. 388), or in Bugaba Island where breeding ground marks the colony centres (p. 423). There can be no super-density of fly except under exactly such conditions as prevailed at Kimmi when there is food generally distributed throughout the island, shelter and breeding ground within easy reach of food, and no opportunity for dispersion. There may be starvation and famine, and a greatly reduced reproductivity, but it cannot be induced by the fly's own activities, unless (1) conditions of life are locally favourable to increase, and (2) dispersion from the locality is arbitrarily restricted.

X. General Conclusions.

There are three specific requisites to life of *Glossina palpalis*, one *sustentative* and two *protective* :—good shelter and breeding ground. One kind of food, the blood of vertebrates, suffices for the insect in all its stages. The two kinds of protection serve adults and pupae respectively.

All these appear equally requisite. There is some slight evidence that other food than blood may be taken, but none concerning its nature, and no evidence that any other is required. There is much evidence that blood is absolutely required—as supplied by the experiment cited in Sect. II (*b*), and the effect upon behaviour of flies of depriving them of their normal food supply; by the apparent reduction in rate of reproduction and in density of fly on Kimmi Island associated with obvious shortage of food (Sect. IX (*h*)); by the long-shore distribution of fly in the Bwendi district as described in Sect. VI (*g*); by the distribution of fly in the Mujuzi Creek district (note to Sect. III (*e*)), and in various other cases. No one of these cases, of itself, would establish the fact, but the cumulative evidence is all to one effect, and the mass of it convincing.

The absolute necessity for the kind of protection that is provided by breeding grounds is particularly well shown by the fly survey of Bugaba Island (Sect. VI (*g*) and fig. 7). This was confirmed by similar surveys of Bubembe and Bunyama Islands, which have not been included herein for the sake of brevity, and by observations many times repeated. It is not requisite that the breeding grounds should be in sand or gravel—fine, dry vegetable debris will serve as well; but it happens that the sand and gravel breeding places are most extensive in this particular region, and more attractive than any other, so that very much the larger number of flies breed in them.

A surprise was the discovery that " massive shelter " is requisite to the life of this fly. This discovery was entirely unexpected, and for a long time it seemed incredible that absence of massive shelter should be the explanation for absence or relative scarcity of fly on the islands cited in Table XXXIII (p. 428). Cumulative evidence finally dispelled all doubts—notably that supplied by the study of the Lutoboka Bay colony (fig. 9, p. 431); by conditions along the southern shore of Buganga Peninsula (Table XXXIV, p. 432); and various other less striking cases not cited in these pages. There could be no doubt, in the end, that the light shelter that is most attractive to the active flies, and which also serves in the majority of cases to shade breeding grounds, is insufficient to protect the inactive flies from destructors, animate or inanimate, as the case may be.

Apart from these things the insect appears to require nothing except that which is inseparable from an equable, tropical climate. It is believed to be pure coincidence that the insect is never found far from water, and it is confidently believed that it would exist, and that it will be found eventually to exist, in any inland localities where host animals of favoured species occur in well sheltered areas provided with suitable breeding places. In fact the interior infestation on Mbugwe Island, described on page 384 and mentioned in several other connections, is believed to be a true inland colony, such as might occur equally well at any distance from lake or river under a comparably favourable (and extremely unusual) combination of circumstances.

The three requisites being equally indispensable, it follows that in the absence of any one the species cannot exist. All three must be present in proper combination, and local density is likely to be governed by the quantity or amount of whichever one of the three is least abundantly provided :—

(*a*) by amount of food, if protection is more than sufficient, relatively ; (*b*) by amount of shelter, if food and breeding ground are both more than sufficient, relatively ; and (*c*) by amount of breeding ground, if food and shelter are both more than sufficient, relatively.

This is indeed the case. In the Bwendi district (Sect. VI (*g*)) shelter and breeding grounds were both very good and extensive, but food was very scanty and density of fly low; along the southern shore of Buganga Peninsula, (p. 432, Table XXXIV) food and breeding grounds were both good and plentiful, but shelter was poor or lacking, and density of fly was therefore low ; on Bugaba Island (p. 424) both food and shelter were good and plentiful, but breeding grounds were poor, or few, and density of fly was low. These are merely specific instances selected to illustrate the general rule, which was upheld everywhere.

A very important question is : What constitutes a proper combination of the requisites to life ? It is obvious that they must occur within the radius of movement and perception of individual insects, from a central point, or from each other ; but this does not answer the question. What is the radius of movement and perception— or it may be called the radius of range or reach—of individual insects ? This question can only be answered empirically, and unfortunately it did not occur to me until nearly the close of the investigations to attempt to answer it. Careful review of field notes, supplemented by memory of conditions not accurately described, leads to the tentative conclusion, that unless all these requisites to life occur within a radius of less than 100 yards from a central point, the conditions of life are so unfavourable that the species cannot exist.

This does not mean that territory deficient in one or more of the requisites to life is never infested. On the contrary, in the major portion of the infested territory conditions of life are unfavourable to the existence of the species, and these portions owe their infestations to their contiguity to territory in which the life requisites occur in proper combination, and which thus becomes a centre of infestation for a considerable zone surrounding. Within these centres natural increase of fly from generation to generation exceeds mortality, but in addition to loss through mortality there is loss through emigration or dispersion of flies into the surrounding zone where conditions of life are positively unfavourable. In this surrounding zone loss through mortality exceeds gain through natural increase, but in addition there is gain through immigration from the centres of infestation. A perfect "natural balance" is thus established and perpetually maintained, so long as flies are free to disperse from the infested centres into the surrounding zone. If dispersion is interfered with, the mechanism of this balance is thrown out of gear; but this very rarely happens in nature so far as I am aware it failed to function in this region only on a few small islands, such as Kimmi, where the conditions of life appear to be so favourable that super-density results at frequent intervals, causing the host animals to abandon the locality temporarily until the density of fly is reduced. Here we have a natural balance constructed on an entirely different mechanical principle, which operates as effectually, but not nearly so smoothly, as in the majority of cases, in which it is the flies and not the host animals that are moved to disperse from over-densely infested localities.

The rôle played by natural enemies and destructive factors generally is to destroy the insects, and to prevent the existence of the species everywhere beyond the limits of dispersion from protected localities. The protection of shelter and breeding grounds suffices against all destructive factors, animate and inanimate, except possibly and very rarely, against extraordinary numbers of spiders or dragonflies. The protective factors in the bionomics of the species are far more specific in their nature, and easily studied, than the destructive. It is, therefore inadvisible to study the destructive factors specifically. It is possible to utilise them for controlling the density of the pest easily enough by merely depriving it of its specific protection against them, but altogether impossible to expect them to penetrate protected precincts, or to utilise them otherwise than in the manner indicated by the facts.

It is possible to argue successfully that the species is normally controlled in range and density by the amount of *available* food, provided that the word "available" is broadly enough interpreted. Food, to be available, must be within reach of the insects from protection (of both sorts). It is also necessary that the host animals should be complacent under attack, for there is no host of the insect which cannot protect itself against attack if it will. Monkeys are "unavailable" as hosts, not because their blood is less suitable as food, nor because the flies are unable to draw it, but entirely because the animals are so active in protecting themselves. Sheep and goats are more complacent and less active in protecting themselves than monkeys, but much less complacent and more actively self-protective than oxen or antelopes. Men vary greatly in temperament, but the average man stands between goats and sheep on the one hand and oxen and antelopes on the other. The large reptiles are the most complacent of all, and most available as hosts, despite the fact that the flies experience measurably greater difficulty in drawing blood from them. Availability of food thus varies greatly with the species, and with the temperament of the individual host, and also with circumstances and conditions of time and place. If large Tabanid flies are annoying oxen, they become less available as sources of food; if *Glossina* itself increases in local density, its host animals become less available. This is strikingly exemplified by human behaviour. If there are very few flies a man pays little or no attention to them, and they have relatively little difficulty in feeding; but if there are very many flies, the man provides himself with one or two fly switches, and they have proportionately greater difficulty in feeding.

Availability of food is also measured by the precise location of host animals with respect to protection. If separated from shelter by as much as 20 yards of unsheltered terrain, food may be entirely unavailable to the flies. This was proved by conditions along certain reaches of shore in Buddu, where there was abundance of crocodiles along a sandy beach separated by from 20 to 100 yards of grass land from shelter and breeding grounds. The flies could not perceive the hosts at this distance, and they do not freely range so far from shelter in search of food.

The factors which operate naturally and control the range and density of *Glossina palpalis* in this region are, mainly, as described above; the factors which can be operated by human effort to reduce obnoxious density to within innocuous limits are identical. It is useless to contemplate destructive control measures. We can see from the experiment and observations made on the "spider islands" that it requires an immense amount of destruction by specific agency to produce a measurable effect on the density of the species. The spiders on Wema Island actually destroyed enormous numbers of flies, but for the most part these flies would have been as promptly destroyed by any one of various other agencies in the absence of the spiders. If the spiders are about, the flies increase to slightly greater density, and then, through wider dispersion, run greater risks and the natural balance is struck at a slightly higher level. Or, stating the same truth in another way, the main effect of artificial or unduly heavy natural destruction of flies by any specific agency is to make conditions of life much more favourable to the rapid multiplication of the survivors. It is wholly impractical to consider any control measures involving artificial destruction of flies, and wholly necessary to rely upon measures designed to deprive the insects of either food or protection or to render food less available to them.

For reasons in part set forth in Sect. II preceding it is regarded as inadvisable and even dangerous to contemplate control of the pest through depriving it of food. It is probable that if completely deprived of all favoured hosts it would be unable to exist on hosts favoured to a no greater degree than sheep, goats and man, but it is probable that it would continue to exist if cattle or pigs were provided. It is also certain that where favoured hosts are plentiful, man is almost immune to attack, but that when they are few man is freely attacked, and our object must always be to protect man rather than to destroy flies.

There is no such objection to the proposition of controlling fly through depriving it of protection, and it is on measures designed to this end that we must chiefly rely. They are the clearing measures already in use, and they have been proved efficacious on many occasions. The maximum of economy and efficiency is to be gained through clearing at precisely the right points—*i.e.*, at the centres of infestation wherein natural increase of fly is most rapid. By clearing these the dispersion of flies into the surrounding zone is prevented, and the effect is general. By clearing in the zone infested by immigrating flies the effect is local at best. A small amount of clearing at the centres of infestation may be much more effective than a large amount of clearing away from them.

It is useless, however, to discuss ways and means for reducing obnoxious density of this pest until some decision has been reached concerning what constitutes obnoxious density. It has been shown by three investigations that the density of infestations by this insect, as measured by the males to be caught " per boy per hour," ranges all the way from less than 0·1 to more than 150·0. A locality is no less truly infested if density is 0·1 than if it is 150·0—the difference is wholly one of degree. We know that a density of 0·1 to 1·0 is innocuous, because density in populated districts along shore appears never to have been reduced below these figures, despite which human trypanosomiasis formerly prevalent—when density was much higher—seems completely to have disappeared. There is good reason to believe that a density of 6·0 is ordinarily safe and sanitary, but that one of 15·0 or 20·0 would ordinarily be dangerous. Admittedly it would be desirable for purely sanitary reasons to reduce density to 0 everywhere, but the expense would be so enormous as to render it completely impracticable. Practical measures must combine efficiency with economy, and the most economical measures are such as do not carry reduction in density of the pest beyond what is necessary for sanitary reasons.

XI. Effect of Fluctuating Lake Level on Glossina palpalis.

In Sect. VII (*e*) mention was made of the effect of fluctuating lake-level on range and density of *Glossina palpalis*. Following are data bearing on this point, which could not well be included in that section, and from which certain conclusions may be drawn, as presented.

XI (*a*). **Fluctuations in Level of Victoria Nyanza.**

Victoria Nyanza is usually highest in May and lowest in November, with a tendency to rise in December and to fall in February. The average yearly fluctuation is about $1\frac{1}{4}$ feet. But the movements are very irregular, and in 1906, instead of falling in February it rose steadily from November 1905 until the following May, and reached an unprecedented height. Again in 1910 it failed to rise in December, but continued to fall steadily until it reached an unprecedentedly low level in February 1911. The maximum in May 1906 was about $4\frac{1}{2}$ feet above the minimum in February 1911, and was nearly 3 feet higher than the maximum from 1911 to 1913 inclusive.

The fluctuations during the ten year period ending in 1913 are shown on a graph recently published by Dr. H. Lyndhurst Duke (Bull. Ent. Res. IX, p. 270).

XI (*b*). **Effect of Fluctuations on Shelter and Breeding Grounds of Tsetse.**

The high level of 1906 uprooted much vegetation along the shores and washed clean the sand and gravel beaches that in 1913–14 lay some 3 feet higher than and anywhere up to 200 yards inland from the foreshore. Following recession of the water, new vegetation sprung up to shade the newly washed sands and gravels, and ideal breeding grounds were created where none, perhaps, existed before. But already in 1913 and 1914 these new breeding grounds were beginning to deteriorate. Leaf-mould was accumulating and covering the sand, vegetation was massing above it and keeping it cold and damp; and already some of these breeding places had become second-rate or quite unattractive. They were fast becoming like the deposits of sand and gravel that lay beyond the flood mark of 1906, which are nearly always hidden from sight beneath blankets of mould and quite valueless as protection to tsetse.

These were the principal changes that were taking place in the conditions of life for tsetse along the lake shore as a result of the flood tide of 1906 and subsequent low water. At some places the changes were of a very different character, and more kinds of changes were progressing than can well be described in detail. In general, however, it can be stated that wherever the shore rises very gradually, and most particularly at the many points where the gradient is less than 1 per cent., extraordinary changes in the conditions of life for tsetse are likely to follow any such unusual flood as that of 1906. But if the land rises sharply from the water the changes may be insignificant, and usually are of no consequence.

In a general way the island survey had shown that the range and density of fly must have been profoundly affected by the movement of the water, but the real extent of the changes wrought was not appreciated until, in 1915, a fly survey was made of the Buddu shore. This region had been surveyed in August and September 1906 by Dr. Van Someren, whose reports were in considerable detail, and permitted the quite accurate comparison which follows.

XI (c). Increase in Density of *Glossina palpalis* due to falling of Lake Level.

The lake shore of the district of Buddu was surveyed for fly in 1906 by Dr. R. Van Someren, working under the direction of Dr. A. D. P. Hodges in the Sleeping Sickness Extended Investigations. This same shore was surveyed by me in 1915, and a most extraordinary change in conditions of infestation was found to have occurred. Following is an extract from the MS. report of Dr. Van Someren, kindly supplied me by Dr. Hodges, paralleled by comments on the present conditions.

Conditions in 1906. (Report of Dr. R. Van Someren.)	*Conditions in* 1915. (Fly Survey.)
"When I came to Bale, a little south of Namirembe I found the distribution again interesting.	
"Northwards from Bale I found the whole coast some 3 miles up to Namirembe devoid of fly, and from Namirembe for some further 2 to 2½ miles, roughly, into the Gwamba also with no fly.	Northwards from Bale the whole coast to Namirembe was found infested to the average density of 6·3. At Namirembe it was very low, but about half a mile beyond the landing it began to increase rapidly, until at points from 2 to 2½ miles beyond it had reached the very high average of 63·5. I have never but twice seen fly more numerous or more annoying (see fig. 11).
"After this point one meets them at first very scantily indeed; then in increasing numbers right up to our limit in the Gwamba some 8 to 10 miles from Namirembe.	After this point the density rises to yet higher figures (76·5, 73·5, 89·5, etc.) and then falls away to moderate figures (5·3, 7·5, 5·5, etc.) but only to rise again later. The average for this 6 to 8 miles of shore is the very high one of 37·6.
"For some 3 miles southward from Bale no fly are met with till a small point near the landing place Sekwe (Calcosa) close to Dumo, where I came across them in small numbers and limited practically to this point.	For some 5 (not 3) miles southward from Bale to Sekwe the shore is continuously infested, and at 3 miles (2 miles north of Kalkosa or Sekwe) is the centre of the Mujuzi Creek colony described on p. 387 and illustrated by figure 5, with the extreme density of 98·0.

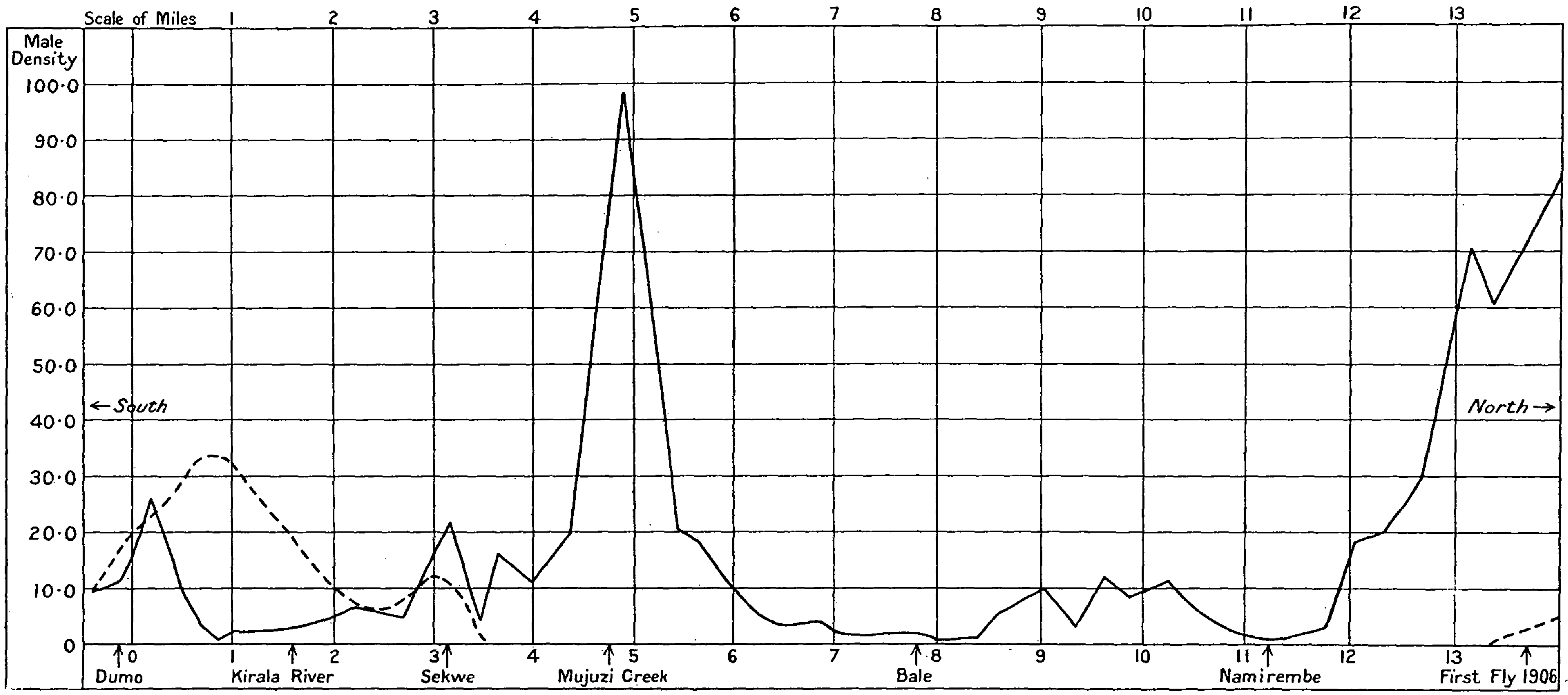

Fig. 11. The dotted line shows the occurrence and density of Glossina palpalis in 1906, and the solid line in 1915.

Conditions in 1906.

(Report of Dr. R. Van Someren.)

"While on one side of the point we caught 8 on the two occasions we waited for them, on the rocks on the other side some 10 yards [rods ?] across, where several men and boys were sitting fishing, we did not observe a single fly about their persons, and amongst a group of some 20 drawing a seine a little further along we caught only one the second day.

"The physical conditions in these sections, starting from our limit in the Gwamba southwards, are as follows:—

"A sandy beach extends practically the whole way, except close to Sekwe, where the trees are practically at the water's edge.

"The land behind is low and covered in parts with scrub; in others with larger trees with here and there wide open areas intervening again. At some portions the tree-covered areas are swampy some distance back from the beach.

"At the fly limit north of Namirembe this swampy part comes quite close to the beach and remains so more or less continuously till close to Bale, and continues thus practically to Sekwe, except for portions here and there where the swamp line again comes close to the beach. In many parts the beach is not so high that during high winds the waves wash right over into the swamp.

Conditions in 1915.

(Fly Survey.)

The density at these points (Sekwe) averaged 9·2 in 1915—probably not far different from that observed by Dr. Van Someren in 1906, except that it applies to the shore in both directions from the rocks. (These are the only rocks for miles in either direction and identify the locality absolutely.)

The physical conditions in these sections have undergone radical changes owing to the falling of the level of the lake.

A sandy beach is practically continuous the whole way except for the reach of two miles north of Sekwe. Here the beach of 1906 is separated from the present shore line by a belt of marsh, very soft and muddy, into which one sinks knee to thigh deep. Outside the marsh are the beginnings of a new beach, very narrow and wet. Outside of this is a hedge of ambatch, or merinde, that only permits passage of canoes inward to the land at a few points. The old beach of 1906, thus completely cut off from the present wa erline, is overgrown with an excessively dense tangle of vegetation. This continues to a point "close to Sekwe" where the trees are still "practically at the water's edge," and (the shore being rocky or falling away steeply) the conditions are virtually unchanged, either physically or, as nearly as can be judged, with respect to infestation by fly.

These conditions are unchanged; there is more of swampy land back from beach than Dr. Van Someren's notes might imply.

The falling water wrought most radical changes in the conditions here described. The beach of 1906 is now high and dry, and there may be 20, 30, 50 or in some places 100 yards of dry sandy embankment between the present beach line and the tree or reed grown swamps and marshes back of it. This almost continuous embankment is partly open in places, and in other places overgrown with dense jungle. Instead of a narrow wet beach with high waves breaking over it, we have a broad sandy embankment with swampy areas "some distance back from the beach," and providing ideal shelter and breeding ground for the fly. It should be added that in 1915 somewhat higher water than for the past few years was working still further changes; building new beaches and cutting off new bits of newly made marsh from the open lake at certain points, and

Conditions in 1906. (Report of Dr. R. Van Someren.)	*Conditions in* 1915. (Fly Survey.)
	cutting away the embankment at others, so that the young trees and jungles growing upon it were being undermined and thrown into the lake.
"A more or less continuous line of merinde trees occurs some 5 to 15 yards off the shore.	The new shore line cannot be less than 20 or 30 yards, average distance, outside the shore line of 1906. The old line of merinde trees has mostly disappeared, with only here and there a few straggling survivors or decaying trunks. A new line, continuous or nearly so for some 3 miles north of Sekwe, has sprung up, and at other points a new line is forming.
"I formed the opinion therefore that the absence of fly from the point north of Namirembe until Bale could be accounted for by absence of suitable breeding places owing to the conformation mentioned.	Certainly the conditions described could not possibly provide good breeding places; neither would the shelter be suitable. Either cause would suffice in explanation.
"Southwards of Bale however the beach is narrower and fringed with small bushes and apparently suitable for fly.	Southward from Bale the beach is now from 20 to 100 yards from bush or forest with open grass land intervening. Then for rather more than a mile thick jungle grows to the very edge of the water. Beyond this it is open or semi-open to Mujuzi Creek.
"I was surprised, therefore, to find none, and cannot account for it.	In 1915 this reach of shore appeared to be foodless, and the flies dispersing into it from the great colony at Mujuzi creek were plainly famishing (88·8 per cent. of females at one point, see p. 373).
"This part of the coast is being gradually encroached upon owing to the action of the waves killing the trees and bushes by washing away the soil, which is chiefly sand. "I repeatedly examined these fly-free areas under favourable weather conditions, but the results were uniformly negative.	This part of the coast is now (1915) being added to, and the conditions described by Dr. Van Someren prevail at points north of Bale, as noted above.

Note on Sex disparity.

"As regards the relative number of male and female flies I have evidence which I think goes to support Dr. Bagshawe's observations (No. 42, S.S.E.I.) as I have had most favourable opportunities for the purpose.

"On three occasions with the aid of the fly boys we examined simultaneously that part of the Gwamba where numerous fishermen were daily working the sambas, and another part some miles beyond the last net where practically only passing canoes may chance to camp the night. The results were:—

Frequented Area.

1st day	52 ♂	to 58 ♀
2nd „	40 ♂	to 37 ♀
3rd „	24 ♂	to 29 ♀

Unfrequented Area.

1st day	75 ♂	to 40 ♀
2nd „	113 ♂	to 68 ♀
3rd „	95 ♂	to 37 ♀

The catch of fly made over approximately this same territory in 1915 consisted of 768 males to 591 females = female percentage of 43·9.

This compares with the following figures of percentages from Dr. Van Someren's report.

Frequented area:—Males 116 to females 124 = female percentage of 51·7.

Unfrequented area:—Males 283 to females 135 = female percentage of 32·1.

Total catch both areas:—Males 399 to females 259 = percentage of females of 39·2.

Dr. Van Someren does not state the number of fly boys employed or time spent in catching, but it is interesting to note that the flies are about as hungry in the general region now as they were in 1906, there being a difference of but 4·7 points between the figure for the total catches at the two widely separated periods.

As will be seen by reference to the graph (fig. 11), the increase of fly in the region south of Bale and just north of Namirembe has been phenomenal. Below Sekwe, however, the reverse has taken place, as shown by comparison between conditions in 1915, and as they were described by Dr. Van Someren in 1906 in his report for that region.

Conditions in 1906. (Report of Dr. R. Van Someren.)	*Conditions in* 1915. (Fly Survey.)
"The only fly met with (in the region south of Sekwe) occurs along the shore from a point near the village of Dumo northward for about one and one-half miles to the Kirala River, and gradually tailing off from this river toward Sekwe.	The fly still occurs from the same point near the old site of the village of Dumo northward, but its density is notably changed at several points.
From Dumo toward the river the fly is very abundant.	The fly is hardly what would be called "very abundant" at any point, but it is not at all abundant from Dumo toward the river. On the contrary, it falls off to a low minimum before the river is reached, and then begins to rise slowly, owing to migration from the colonies at Sekwe and Mujuzi Creek. The infestation at the Kirala River now consists mainly of flies coming in from Sekwe, instead of being at the edge of a centre of infestation with fly tailing off toward Sekwe.
"The range inland (between Dumo and the Kirala river) is practically nil, as the extent of dry land at the lake-side is not more than five yards in width at the broadest part. Inside this dyke is extensive dense forest of kibo palm (*Raphia*) down to the lake-side, standing in very swampy ground.	The extensive dense forest still exists, and is still exceedingly swampy, the water at the back of the dyke standing at a higher level than the lake. But instead of coming down to the lake-side there is a belt of exceedingly soft marsh, with grass and a little papyrus lying outside the old beach, from which the open lake is all but completely hidden. The dyke, or beach of 1906, is now a terrible tangle of shrubbery weighted down with rank vines, and with marsh grasses growing rankly along its outer edge. Outside the marshy belt, 10 to 30 yards from the old beach line of 1906, a new beach was forming in 1915. Range inland at this point is noted on page 408. Flies were found on a situtunga shot 400 yards from the lake shore.
"Opposite Dumo, where the ground rises fairly sharply the fly crosses a belt of scrub and long grass intervening between lake and village and is found in the plantations immediately bordering the belt. I frequently saw them on women digging in this part.	At the very end of the fly beach described by Dr. Van Someren, where the ground begins to rise fairly sharply, is found the remains of the large colony he describes as existing in 1906. A few hundred yards south the belt of scrub and tall grass—elephant grass—still separates the lake from what were the old plantations. There is now exceedingly dense jungle with occasional openings kept clear by the hippo and permeated with a net work of hippo trails. The fly still penetrates the belt of tall grass, following the hippo trails, which have replaced the foot-paths leading to watering places, and it is now found inland, in the very centre of the old village site (see p. 408 note on inland range at Dumo).

Conditions in 1906.	*Conditions in* 1915.
(Report of Dr. R. Van Someren.)	(Fly Survey.)
"Just beyond Dumo there is again a forest area for some half mile. Where the forest ceases until the German boundary there is no fly to be found.	The fly stops at a point only 100 yards beyond that indicated by Dr. Van Someren. But there are several colonies south of the point.
"Of the flies caught in this area 187 were males and 72 females (= 28 per cent. females).	The total catch in this area was 215 males and 184 females, making 46 per cent. females.
"At Dumo by one of the watering places I caught 20 females to 14 males (= 59 per cent. females).	At the identical watering place (the only one in the fly area) two catches were made on different days as below :—
"On another occasion along the forest up to the Kirala River my boys caught 106 males to 2 females (= 1·9 per cent. females). This is of interest in connection with the physical features. Since fibre collecting ceased there practically no one visits it.	Along the forest up to the Kirala River the catch of males was identical, 106, but that of females was 86, making 45 per cent ♀.

Males.	Females	Female percentage.
15	41	73%
19	57	75%
34	98	74%

Again it is interesting to note that sex ratio shows that the watering place, which is (or was) just outside the "belt of scrub and long grass," is now, as it was in 1906, unattractive to the idle males, and is the point south of the colony centre where female percentage is highest. But northward, along the beach where "practically no one" went in 1906, the conditions are absolutely changed.

The foregoing brings out clearly the need for eternal vigilance if any systematised effort is ever made to repopulate the riparian zone and islands, and to protect the population against recurrence of sleeping sickness. There is no more dangerous reach of shore in Africa, perhaps, than that between the points Sekwe and Bale, yet it was perfectly safe apparently in 1906, and the changes have been wrought by the falling of the lake level.

Wherever the shore falls gradually into the lake, similar changes are likely to occur at any time, especially if there is much sand in the district. The danger points can be found by a "fly survey" of the shore, and must be watched to preclude the chance of conditions eminently favourable to spread of the human parasite coming about unknown to sanitary or administrative officials.

XI (*d*). Causes for Fluctuation in Lake Level.

Causes for the irregular fluctuation in level of Victoria Nyanza are, in part, its great size and narrow outlet. From so great an area loss through evaporation must be enormous, and relatively constant as compared with the overflow. The latter represents the surplus of rainfall over evaporation, and if evaporation is a relatively constant quantity, any variations in rainfall are likely to be greatly exaggerated. The surplus not being so very large, it does not require much to double it.

The narrow outlet to the enormous volume of the lake acts like a choked safety valve. Rise in lake level may be very rapid, but fall is more gradual. It seems to have required more than a year for the unusual surplus that gathered so quickly in 1906 to find its way through the walls of rock at the source of the Victoria Nile. If the outlet were not choked in this manner the level of Victoria Nyanza would be somewhat more constant, and the flow of the Victoria Nile somewhat more variable. If it were yet more effectually choked the flow of the river would be more constant and the level of the lake subject to yet wider fluctuations.

XI. (*e*). **The probable Effect of a Dam at the Outlet upon the Tsetse along the Shores of Victoria Nyanza.**

The outlet to the lake into the Victoria Nile is a superb source of water-power, and one of Uganda's great assets. The topography permits its relatively cheap development. There is a natural dam, and excellent opportunity for a canal along the eastern shore of the river, which does not immediately fall away. But a dam would permit a much more complete utilisation of the power that it is as certain to be built as that the economic development of the country will continue.

It is neither a high nor a low level of the lake that creates favourable conditions of life for tsetse, but a fluctuating level. The rising waters clear away massed vegetation and wash clean the breeding grounds ; the falling waters permit the growth of new shelter and the breeding of fly in the renovated terrain. Continued growth chokes the breeding grounds, and hides them beneath massed vegetation or the accumulations of mould.

If a dam at the outlet of the lake could be so constructed as to equalise the level of it by permitting more rapid egress of rising waters, it might have a beneficial effect in reducing the density of tsetse along its borders. But the object in building a dam would be the very opposite ; it would be to equalise the flow of water in the power canal and the Victoria Nile, and thus to accentuate the fluctuations of the lake.

This might, conceivably, be prejudicial to the fly below the dam, but it would be beneficial to fly above it.

It would be delightful if construction of a dam, and utilisation of the water-power at the source of the Nile could be urged as a sanitary measure, but unfortunately its construction will have the opposite to the desired effect.