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Host Preference in *Aedes (Stegomyia)* Mosquitoes in Uganda. II. Studies on Indoor and Outdoor Biting and Resting Behaviour with Special Reference to *Aedes aegypti* L.

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Abstract

Field studies on the resting, breeding and feeding behaviour of *Aedes aegypti* L. in Uganda have shown that this mosquito is exophagic and exophilic in this area. Studies on the response rates of the endophilic and exophilic strains of *Ae. aegypti* in a Gouck olfactometer have indicated that the response rate of Ilobi strain is about 39% and that of Bwayise is about 18% in a period of three minutes. In *Aedes simpsoni* Theo., however, the response rates for exophilic Bwamba and Bwayise strains are 6 and 7 percent respectively; and that of *Aedes vittatus* Bigot is 1.4 percent. The higher response rate of Ilobi strain correlates with its endophilic behaviour. Host preference results have indicated that the findings are as a whole in conformity with what is known of these strains with the exception of *Ae. vittatus* and Bwamba *Ae. simpsoni* which appear to be reversed to zoophilism. Reduction of light intensity in the test chamber, or of the access slit to it, depressed the response of all strains equally suggesting that these cues are not important in determining the observed difference between endophilic and exophilic strains under those conditions. Anomalies in host preferences under the experimental conditions used suggest, however, that the olfactometer may be unsuitable for behavioural experiments on exophilic species.

Introduction

Some mosquito species feed and rest exclusively outdoors (exophagic and exophilic), some indoors (endophagic and endophilic) and still others in both situations (SENIOR-WHITE, 1954). More and more observations tend to show that the behaviour of mosquitoes with respect to feeding and resting habits is subject to considerable variations which may or may not be attributed to climatic differences. In Uganda, for example, *Aedes aegypti* L. appears to be exophagic and exophilic whereas at the East African coast at least three behavioural forms are found: an exophagic and exophilic form, an endophagic and endophilic form and an intermediate form (TEESDALE, 1955; VAN SOMEREN et al., 1958; MATTINGLY, 1957; MCCLELLAND, 1960). In the *Anopheles gambiae* complex a similar intraspecific variation has also been observed (HADDOW, 1945; HOLSTEIN, 1954; GILLIES, 1956; HADDOW & SSENKUBUGE, 1973). It appears that in species where there is intraspecific variation for these behavioural characters, endophagy and endophilism

are generally associated with anthropophilism; and exophagy and exophilism are associated with zoophilism (HEISCH et al., 1959, MCCLELLAND, 1963). GOUCK (1972) working on the Newala strains of *Ae. aegypti* in Tanzania, found that the indoor strain is highly anthropophilic and the outdoor one exhibits zoophilic tendencies. It should be noted, however, that in species where there is no intra-specific variation in exophilism and endophilism and/or exophagy and endophagy, exophilic species can either be anthropophilic or zoophilic as in *Aedes simpsoni* Theo. (GILLETT, 1951, 1955; MUKWAYA, in press). Although such inter-specific and intraspecific variations have been observed in mosquitoes, the basis for these differences has not been determined largely due to the absence of a practical laboratory technique. HOLSTEIN (1954) postulated a possible existence of exophilic and endophilic biological races in *A. gambiae;* but GILLIES (1956) argued that in the absence of critical morphological differences between the two such populations, demonstration of their existence would be very difficult. It is possible, however, to devise a behavioural laboratory technique which can distinguish the two forms without necessarily refering to morphological differences as was done for host preference in *Ae. simpsoni* (see MUKWAYA, 1971). The purpose of this paper is threefold: to present evidence that Uganda *Ae. aegypti* is exophagic and exophilic; to provide a technique which can distinguish between the outdoor and indoor forms in the laboratory and to attempt to determine the behavioural correlates of exophilism and endophilism in at least *Ae. aegypti.*

Definition of terms

The following terms are frequently used with regard to feeding and resting behaviour of mosquitoes and for more details one should consult SENIOR-WHITE (1954) and GILLIES (1956):

1. Endophily, the habit of remaining within a man-made shelter throughout the whole or a definite part of the gonotrophic cycle (indoor resters).
2. Exophily, the habit of spending the greater part of the gonotrophic cycle out of doors (outdoor resters).
3. Endophagy, the habit of obtaining a blood meal within a man-made shelter.
4. Exophagy, the habit of seeking a blood meal out of doors.

Materials and Methods

Experimental mosquitoes, their host relationships and behaviour

Three strains of *Ae. aegypti* were used: The Ilobi strain which originated from Nigeria and has been maintained in this laboratory as a colony for over 15 years. It is endophagic and endophilic; and anthropophilic even in the wild (KERR, 1933). In order to get biologically meaningful results, this strain was supplemented with another strain from the East African coast which was reared in the laboratory for only 7 generations. It is also anthropophilic, endophagic and endophilic. The third strain was a local strain (type *formosus*) from Kampala, the capital of Uganda and was reared in the laboratory for seven generations. It is believed to be exophagic and exophilic, and it has zoophilic tendencies (MCCLELLAND, 1963; MUKWAYA, 1971).

In order to test the efficacy of the technique, two other species which are known to be exophagic and exophilic were also tested: Two strains of *Ae. simpsoni;*

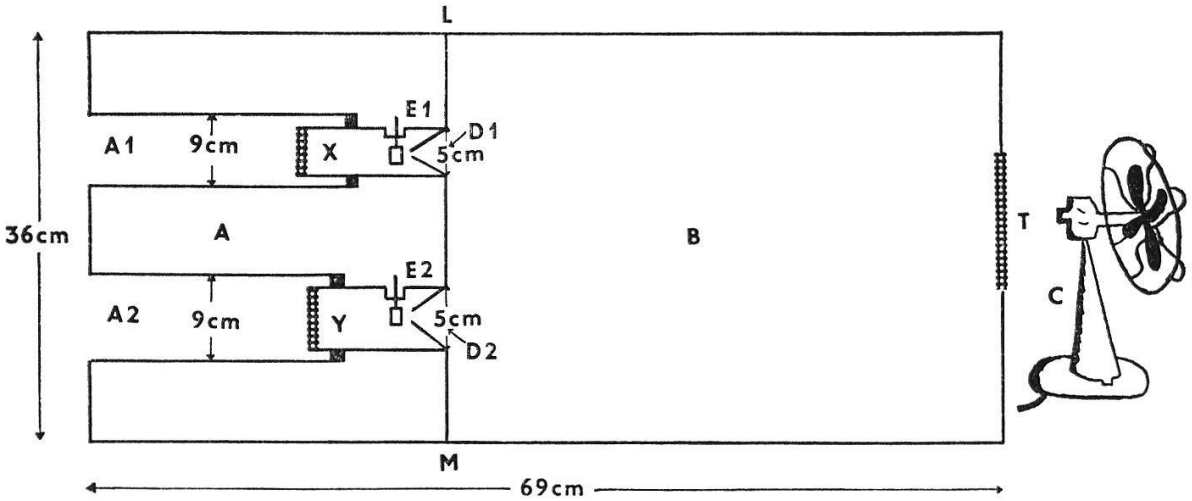

Fig. 1. GOUCK's type of olfactometer.

the anthropophilic Bwamba strain and the zoophilic Kampala strain (GILLETT, 1951, 1955 and MUKWAYA, 1971). These strains were reared in the laboratory for only one generation because of the difficulty of mating these strains in captivity. *Ae. simpsoni* was therefore supplemented by *Aedes vittatus* Bigot strain which is strongly anthropophilic; and bites and rests outdoors. It was reared in the laboratory for seven generations.

Field studies on exophilic and endophilic behaviour of *Ae. aegypti* in Uganda

In areas where *Ae. aegypti* is endophilic, it may also breed indoors. Surveys of larvae and resting *Ae. aegypti* were, therefore, made in selected localities both indoors and outdoors. Further, ten 12-hour human-baited catches inside and outside houses were done simultaneously at selected sites. Two catchers were positioned in a house and two others in plantations near the house. The method of catching was described by HADDOW (1954). Resting mosquitoes were also surveyed both inside houses and outside in plantations. The outdoor ones were collected with hand-nets by disturbing plants in which they rested. Inside houses, sucking tubes were used to catch resting mosquitoes.

Testing for the response rate of *Ae. aegypti, Ae. simpsoni* and *Ae. vittatus* strains in a Gouck's olfactometer

GOUCK's (1972) type of olfactomer (Fig. 1) used in determining host preference in mosquitoes was employed. The olfactometer (36 × 69 cm) was constructed from perspex, an acrylate polymer, and has three chambers: A test chamber (A), a mosquito chamber (B) and a fan (C). A known number of 5–6-day-old mosquitoes, previously fed on sugar, was placed in the mosquito chamber through an opening in the mosquito netting T by means of a sucking tube. Funnel-shaped entrances D_1 and D_2 of about 5 cm each, were kept closed by slides E_1 and E_2. The mosquitoes were allowed to rest overnight. The number of dead or escaping mosquitoes was recorded before each test so that the exact number in the mosquito chamber was known.

The hosts used were a local rat, *Arvicanthis niloticus* Demarst and a human hand. They were inserted into tubes A_1 and A_2 to be sources of odour stimulus and were alternated at equal intervals. After the fan (C) was started, entrances D_1 and D_2 were opened by sliding E_1 and E_2. A slow current of air was, therefore, drawn over the hosts through A_1 and A_2 into B. The mosquitoes in B could make their way towards the source of odour after being exposed to the alternative response. They were eventually trapped in either tube X or Y through D_1 and D_2. The mosquitoes trapped in X and Y were removed by means of a sucking tube through openings made in the mosquito netting at the end of X and Y. Tubes X and Y were then closed. Afterwards tubes X and Y were cleaned with moist cotton wool, mopped with alcohol and allowed to dry.

Two trials at 1400 and 1700 hours in the case of *Ae. aegypti* were done a day, and in the case of *Ae. simpsoni* at 1000 and 1500 hours; *Ae. vittatus* was tested once a day at 2100 hours during which periods the species were expected to be active. The response rate to the two hosts was calculated by expressing the total number of mosquitoes in A_1 and A_2 during the period of three minutes as a percentage of the total number of mosquitoes in the mosquito chamber.

Effect of light and/or slit size on the response rate of strains of *Ae. aegypti*

It was expected that a day-biting exophilic strain would be reluctant to move from the mosquito chamber into the test chamber if the latter had reduced amount of light. Differences in light intensities between the test and mosquito chambers were obtained by covering the test chamber with a translucent tracing paper which diminished the amount of light in this chamber. Further amount of light was reduced in the test chamber by covering it with a black cloth, leaving side LM covered with a translucent paper so that some light could get into the test chamber. The idea was to simulate the natural environment where endophilic day-biting *Ae. aegypti* moves from outside to inside houses where the light intensity is lower than that preferred by the exophilic strain. The olfactometer was illuminated by tungsten bulbs of 60 watts and 100 watts, one bulb being used at a time. The light intensity was measured by a photo-sensitivity thermopile. 400 mosquitoes were tested for the response rate against each ratio of light intensities.

The size of slits through which the mosquitoes pass into the test chamber, could also affect the response rate particularly of the exophilic strain which normally feeds in the open air. The slits were, therefore, reduced to 1½ cm and the mosquitoes tested first with equal light intensities between the mosquito chamber and test chamber and then with reduced light intensities in the test chamber.

Results

Endophilic and exophilic behaviour of *Ae. aegypti* in Uganda

The results for the survey of resting mosquitoes both indoor and outdoor in different sites round Kampala City are shown in Table 1. Not a single mosquito was found inside houses. More males were found resting outdoors than females and approximately two thirds of the total

Table 1. Surveys of outdoor and indoor resting *Aedes aegypti* in and around Kampala city

Site	Outdoor resting *Ae. aegypti* male	female	Total	Indoor resting *Ae. aegypti* male	female	Number of houses surveyed
Kibuye	17	15	32	–	–	10
Mengo	48	19	67	–	–	20
Matugga	20	7	27	–	–	40
Natete	20	12	32	–	–	5
Bwayise	30	4	34	–	–	15
Kisubi	6	8	14	–	–	6
Sisa	43	22	65	–	–	8
Luzira	59	31	90	–	–	10
Namalere	36	8	44	–	–	5
Gayaza	5	4	9	–	–	3
Mukono	23	15	38	–	–	4
Najanankumbi	18	12	30	–	–	12
Lungujja	6	8	14	–	–	7
Total	331	165	496	–	–	145

collection were males. This could be due to the fact that the females have got other resting places different from those of the males or have other resting places different from those of the males or that this strain of *Ae. aegypti* has a distorted sex ratio (see HICKEY, 1965).

Endophagic and exophagic behaviour of *Ae. aegypti* in Uganda

The results for the human baited catches both indoor and outdoor are shown in Table 2. Out of 10 human baited catches only 3 mosquitoes were taken landing/biting inside houses whereas outside houses 251 were taken landing/biting on man.

The breeding behaviour of *Ae. aegypti* in Uganda

The preliminary results for larval surveys both inside and outside houses in different localities are shown in Table 3. Only three larvae were found inside houses and in two distant localities. Almost in all cases, no larvae were found in water containers inside houses. In a pilot study, three tyres were placed inside a house and the same number outside with water. After three weeks many larvae were found in the tyres outside and not a single larva in the tyres inside the house.

Table 2. Human-baited catches inside and outside houses at different sites in Kampala city area

Catch number	Number taken inside house	Number taken outside house
1	–	3
2	–	5
3	–	25
4	2	18
5	1	35
6	–	38
7	–	39
8	–	35
9	–	37
10	–	16
Total	3	251

Table 3. Surveys of *Aedes aegypti* larvae inside and outside houses in different localities

Locality	Larvae of *Ae. aegypti* outside house	Larvae of *Ae. aegypti* inside house	Number of houses surveyed
Kabasanda	++	none	10
Bujongolo	++	none	8
Matugga	++	2	20
Kiganda	++	1	10
Mbirizi	+	none	7
Gombe	++	none	5
Lwemwedde	+	none	8
Masulita	++	none	10
Busunju	++	none	9
Mitalamaria	++	none	3

++ = Many larvae present; + = present but not many.

The response rates of strains of *Ae. aegypti, Ae. simpsoni* and *Ae. vittatus*

The results of the response rates for the endophilic and exophilic strains of *Ae. aegypti* are shown in Table 4. The average response rate for the Ilobi strain is approximately 39 % during a period of three minutes. The results also indicate that approximately 61 % of the responding mosquitoes prefer man to *A. nicolicus*. In the case of the

Table 4. The response rate of strains of *Aedes aegypti, Aedes simpsoni* and a strain of *Aedes vittatus* in Gouck's olfactometer

Species	Strain	Total number of mosquitoes tested	Number of trials	Total number of mosquitoes responding to man	Total number of mosquitoes responding to rat	Total number responding to man and rat	Total average % response
Aedes aegypti	Ilobi	3,075	8	735	470	1,205	39.20
Aedes aegypti	E. A. Coast	3,150	8	724	485	1,210	38.41
Aedes aegypti	Kampala	2,983	8	178	368	546	18.30
Aedes simpsoni	Bwamba	2,952	10	34	130	164	5.56
Aedes simpsoni	Kampala	2,976	10	24	198	22	7.45
Aedes vittatus	Mukono	2,960	10	19	21	40	1.35

Table 5. Effect of light and/or slit size on the response rates of Ilobi and Bwayise strains of *Ae. Aegypti*

Slit size		5 cm			1½ cm		
Light intensity in lumens per sq. meter	Mosquito chamber	18	17.2	17.2	322.20	322.20	3,759
	Test chamber	322.20	322.20	3,759	322.20	53.70	537
Response rate of Ilobi *Ae. aegypti*		322.20	53.70	537	12.1	11.7	7.6
Response rate of Bwayise *Ae. aegypti*		38	37.4	38	7.8	8	2.1

Bwayise (Kampala) strain of *Ae. aegypti* the average response rate is approximately 18 %. Approximately 69 % of the responding mosquitoes showed preference for *A. niloticus*.

The results for the Bwamba anthropophilic strain of *Ae. simpsoni* are shown in Table 4. The average response rate is approximately 6 %. In the case of Bwayise *Ae. simpsoni* the average response rate is approximately 7 %. The results on host preference in both strains indicate that *A. niloticus* is preferred to man. In nature Gillett found that Bwamba *Ae. simpsoni* readily feeds on man (MAHAFFY et al. 1942), and in the laboratory the author, using another technique, has shown them to be strongly anthropophilic. The average response rate for *Ae. vittatus* is 1.4. The few mosquitoes which respond seem to show preference for a rodent.

Effect on light and slit size on the response rate of *Ae. aegypti*

The results shown in Table 5 indicate that slit-size and/or lower light intensity in the test chamber have no marked effect on the ratio

of responders between the Ilobi endophilic and the Bwayise exophilic strains of *Ae. aegypti*. The total number of responders, however, is reduced in both cases, if the size of the slits is reduced.

Discussion

The results on resting, breeding and biting habits of *Ae. aegypti* indicate that in Uganda, at least in some parts, this mosquito is exophilic and exophagic. The three larvae which were collected inside houses, could have been transported in the water from the drums outside to the pots inside the house. The few mosquitoes caught landing/biting inside houses are probably expected as it is rare for behavioural traits to be absolutely rigid. In many other places, for example, *Ae. aegypti* bites, breeds and rests inside houses (KERR, 1933; BONNE-WEPSTER, 1954; MACDONALD, 1956; MCCLELLAND, 1960 and SHEPPARD et al. 1969). Whether this difference in behaviour is innate or related to the availability of hosts, is not yet established. Observations so far seem to indicate that indoor strains of *Ae. aegypti* tend to be anthropophilic and outdoor ones zoophilic (see HILL, 1921; MAHAFFY et al. 1942; HEISCH et al. 1959; MCCLELLAND, 1963; GILLETT, 1971 and MUKWAYA, 1971).

Laboratory studies indicate that the two strains of *Ae. aegypti* are significantly different ($P < 0.01$) with respect to the response rate in Gouck's type of olfactometer. In *Ae. simpsoni,* both strains have approximately the same response rate which is much lower than even the Bwayise strain of *Ae. aegypti*. MUKWAYA (1972) found that *Mansoni metallica* Theo. did not respond at all in this olfactometer. The reason for the poor response rates could be that the mosquitoes are not interested in the hosts in the test chamber, but this is unlikely, as the Bwayise strain of *Ae. simpsoni* is known to feed on rodents (MUKWAYA, 1971), and the Bwamba strain readily feeds on man. The higher response rate of Ilobi correlates with its endophilic behaviour which probably enables it to adapt more easily to the artificial conditions of the olfactometer. On the other hand, the lower response rate of Bwayise *Ae. aegypti* and even much lower response of *Ae. simpsoni* and *Ae. vittatus* correlate with their exophilic behaviour, and this might be the reason why they appear not to adapt easily to the artificial conditions of the olfactometer. In nature, however, a few Bwayise *Ae. aegypti* have been observed inside houses whereas *Ae. simpsoni* is exclusively exophilic; and this could be the reason why Bwayise *Ae. aegypti* has a higher response rate than *Ae. simpsoni* although both are classified

as exophilic. Failure of *Aedes africanus* Theo. (HADDOW et al. 1948) and *Ae. simpsoni* (MUKWAYA, in press) to enter baited cages or traps in the field could also be due to these mosquitoes being exophilic. Thus, the relative response rate of the species tested in the olfactometer seems to correlate with their known endophilic/exophilic tendency, and could be used as a measure of it.

The behavioural correlates of exophilism and endophilism in mosquitoes are not known, and the olfactometer set-up for their investigation failed to give any indication. It was thought that differences in preference for light intensities or tolerance in restricted apertures might characterize the two behavioural forms. Endophilic strains of day-biting mosquitoes feed inside houses where the light intensity is lower and exophilic strains feed in the open air where the light intensity is higher. Similarly, endophilic strains pass easily through small openings into houses where the light intensity is lower than outside. Studies on the effect of light and/or the size of the slits have indicated, however, that neither of the two factors as replicated in a Gouck olfactometer determine the behavioural differences in the two strains of *Ae. aegypti.* Presumably intrinsic factors are involved, since the behavioural differences persist in culture.

The results show a further disparity which suggests that behaviour in the olfactometer is not necessarily indicative of the wild state. The findings on host preference in *Ae. aegypti* are in conformity with what is known of these strains though the degree of zoophilism in the Bwayise strain is much higher than previously found with other techniques (MUKWAYA, 1971). For *Ae. simpsoni* and *Ae. vittatus,* however, there is a discrepancy. *Ae. vittatus* and the Bwamba strain of *Ae. simpsoni* which are known to be strongly anthropophilic in the wild and under other artificial conditions were unexpectedly found to be zoophilic in the olfactometer. This discrepancy could reflect inhibition by the conditions prevailing in the olfactometer. As *Ae. simpsoni* is strongly exophilic and probably also *Ae. vittatus,* their poor response in an enclosed chamber might affect their feeding behaviour; further, the few mosquitoes which respond may not be enough to determine genuine host preference. Hence, use of Gouck's olfactometer for testing host preference in exophilic species of mosquitoes should be made with caution.

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Zusammenfassung

Felduntersuchungen in Uganda über das Brut-, Ruhe- und Nahrungsaufnahme-Verhalten von *Aedes aegypti* L. zeigten, daß diese Mückenart in den betreffenden Gebieten exophag und exophil ist. Reaktionsprüfungen im Gouck Olfaktometer mit endophilen und exophilen *Aedes aegypti*-Stämmen ergaben, für eine Versuchsdauer von drei Minuten, eine Reaktionsrate von ca. 39 % für den Ilobi- bzw. von etwa 18 % für den Bwayise-Stamm. Dagegen betrugen die Reaktionsraten bei *Aedes simpsoni* Theo. 6 % für den exophilen Bwamba-, bzw. 7 % für den exophilen Bwayise-Stamm. Für *Aedes vittatus* Bigot betrug der entsprechende Wert 1,4 %. Die höhere Reaktionsrate des Ilobi-Stammes entspricht seinem endophilen Verhalten. Diese Resultate stehen in gutem Einklang mit den Beobachtungen über die bevorzugten blutspendenden Wirte; Ausnahmen bilden *Aedes vittatus* sowie der Bwamba-Stamm von *Aedes simpsoni,* welche zur zoophilen Lebensweise übergegangen zu sein scheinen. Eine Erniedrigung der Lichtintensität in der Untersuchungskammer, oder auch im Eingangsschlitz, reduzierte die Reaktionsrate bei allen Stämmen; dies läßt darauf schließen, daß der Lichtfaktor unter den angewandten Versuchsbedingungen für das unterschiedliche Verhalten bei endophilen und exophilen Stämmen nicht maßgebend ist. Unübliches Verhalten bei der Bevorzugung verschiedener blutspendender Wirte weist allerdings darauf hin, daß der Olfaktometer für Verhaltensuntersuchungen an exophilen Arten untauglich sein könnte.

Résumé

Des études de terrain sur les comportements de repos, de reproduction, et de nutrition chez *Aedes aegypti* L. en Ouganda ont montré que cette espèce est exophagique et exophile dans cette région. Des études sur les taux de réponses des souches exophagiques et exophiles de cette espèce dans un olfactomètre de Gouck indiquent que le taux de réponse pour 3 minutes est d'à peu près de 39 % chez la souche Ilobi et de 18 % chez celle de Bwayise. Chez *Aedes simpsoni* Theo, pourtant, les taux de réponses pour les souches Bwamba exophiles et les souches Bwayise sont respectivement de 6 et de 7 %, quant à celui de l'*Aedes*

vittatus Bigot, il est de 1,4 %. Le taux de réponses plus élevé pour la souche Ilobi correspond à son comportement endophile. Des résultats sur la préférence d'hôtes révèlent que tous ces résultats sont conformes en leur ensemble à ce qu'on sait déjà sur ces souches: Partout *Ae. vittatus* et *Ae. simpsoni* Bwamba semblent être retournés au «zoophilisme». Une réduction de l'intensité lumineuse dans la chambre expérimentale – ou de sa fente d'accès – a diminué les réponses de toutes les souches, de manière comparable. Ceci suggère que ces faits ne sont pas si importants pour déterminer la différence observée entre les souches endophiles et exophiles dans de telles conditions. Les anomalies enregistrées dans la préférence des hôtes dans les conditions expérimentales décrites mettent en doute l'efficacité de l'olfactomètre pour l'étude du comportement d'espèces exophiles.