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Mosquitoes of Zika Forest, Uganda: Species Composition and Relative Abundance

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Abstract

Mosquito collections were conducted in Zika Forest near Entebbe, Uganda from July 2009 through June 2010 using CO₂-baited light traps, ovitraps and human-baited catches. A total of 163,790 adult mosquitoes belonging to 10 genera and 61 species were captured. Of these, 24 species (39%) were captured in Zika Forest for the first time. All the new records found in the forest in this study had previously been captured in other regions of Uganda, implying that they are native to the country and do not represent new introductions. Twenty species previously collected in Zika forest were not detected in our collections and this may suggest a change in the mosquito fauna during the past 40 years or variation in species composition from year to year. Arboviruses of public health importance have previously been isolated from more than 50% of the 61 mosquito species captured in Zika forest which suggests a high potential for transmission and maintenance of a wide range of arboviruses in Zika Forest.

Keywords

Zika Forest; Uganda; Mosquito Species Composition; Arbovirus Vectors

INTRODUCTION

Investigations of the mosquitoes of Zika Forest near Entebbe, Uganda were initiated in 1946 (Kirya et al. 1977) following a human yellow fever (YF) sero-survey (Sawyer and Whitman 1936) which showed that YF was endemic throughout Uganda. The investigations intensified in 1960 when a 36.6 m (120 ft) steel tower was relocated from Mpanga Forest to Zika Forest to study the vertical stratification of mosquito activity, especially the important sylvan yellow fever virus (YFV) vector *Aedes (Stegomyia) africanus* Theobald (Kirya et al. 1977). In the course of these investigations, the mosquito species composition for Zika Forest was described (Haddow et al. 1964, Corbet 1964). In addition, a wealth of information was gained on the biology, biting behaviour and oviposition activity for the

different sylvan species. Lastly, several arboviruses were isolated from the mosquitoes collected in Zika Forest including Zika virus (Haddow et al 1964b), Uganda S virus (Dick and Haddow 1952) and YF (Kirya et al. 1977) which demonstrated the medical importance of some mosquito species in Zika Forest and enhanced our understanding of the transmission and maintenance cycles of these arboviruses.

The routine mosquito collections at Zika Forest were discontinued in the early 1970s, and the mosquito species composition records have not been updated for more than 40 years. Forty years ago Zika Forest was isolated from all human settlement and virtually unaffected by human activities. Currently, Zika Forest is surrounded by new homes and/or crop fields and plantations and the ecosystems adjacent to the forest have significant modifications as a result of human activity. Studies have shown that forest modification and clearing have a negative impact on biodiversity (Chazdon et al. 2009, Nichols et al. 2007, Koh 2007, Gardner et al. 2008). These studies reported that protected areas are influenced directly or indirectly by many land uses including; road construction, hunting, cattle grazing, agricultural incursions and over harvesting of non-timber products. All land uses around the forest greatly exploit the forest habitat and indirectly affect the mosquito community. These effects have been further compounded by the ever changing climate around the country. The aim of this study was to describe the current mosquito species composition in Zika Forest and compare it to what was observed in the past.

MATERIALS AND METHODS

Study area

Zika Forest is a small isolated tropical forest located between coordinates (32° 30' E and 0° 7' N) and approximately 6 km (3.7 mi) from Entebbe. Zika Forest is a property of the Uganda Virus Research Institute, Entebbe (UVRIE) and it is protected and restricted to scientific research activities. The forest covers approximately 25 hectares (61.8 acres) and forms part of a narrow sinuous strip skirting the extensive grass and papyrus swamps of Waiya Bay, a sheltered inlet of Lake Victoria near Entebbe (Fig. 1). There is a 36.6 m (120 ft) steel tower located within the forest that was set up in 1960 to study the stratification of mosquito activities especially the principal YFV sylvan vector *Ae. africanus* (Kirya et al. 1977). Zika Forest is particularly suitable for mosquito work because it combines several ecosystems including hill-slope forest and very wet swamp-forest which comprises of a wide variety of mosquito habitats (Corbet 1961) and it is easily accessible; only 6 km from UVRIE.

Sampling

Mosquitoes sampling was conducted from July 2009 through June 2010 and the mosquitoes were collected following 3 different sampling protocols. In the first protocol we collected mosquitoes at different heights in the forest from 6.1 to 36.6 m (20 – 120 ft) above the ground. These studies were conducted on the steel tower. In the second and third protocols mosquitoes were collected at the ground level, approximately 1 m above the ground. In the second protocol collections were conducted at different locations inside the forest and in the third protocol mosquitoes were collected along the forest edge. Three different methods

were used to collect mosquitoes, carbon dioxide (CO₂)-baited CDC-light trap and human landing collections were conducted weekly throughout the sampling period, and ovitrap collections were conducted once every 3 months. Eggs collected by the ovitraps were reared to adults and identified to species. All identifications were conducted by using the keys of Edwards (1941), de Meillon (1947), Gillett (1972), Gilles and Coetzee (1987) and Jupp (1996). Climate parameters including temperature, rainfall and humidity were recorded at each time of sampling. Rainfall and temperature data was obtained from a weather station at Kisubi, located approximately 500 m (0.3 mi) from Zika forest. The relative humidity was measured by using a thermometer hygrometer (Viking AB, Sweden).

Statistical analysis

Analysis for mosquito composition was done using the program R 2.10 (R Development team 2010) and Past (Hammer et al. 2001). Differences in abundance of mosquitoes during the year were evaluated using non-parametric multivariate analysis of Variance (NPMANOVA) and the SIMPER test (Analysis of Similarity and Differences between Sites). Means were compared by (NPMANOVA) and when significantly different, they were exposed to the SIMPER test for the analysis of differences between mosquito species in the months and sites. Correlations between temperature, rainfall, relative humidity and numbers of mosquitoes collected over the year and sampling sites were determined using non parametric (Pearson-product moment) correlation analysis.

RESULTS

A total of 163,790 adult mosquitoes belonging to 10 genera and 61 species were collected (Table 1). The highest proportion of the collections were from CDC light traps (97.8%), followed by human landing catches (1.28%) and ovitraps (0.95%). Of the 61 species collected, 56 were collected using CDC light traps, 24 in ovitraps and 9 in human landing catches. Six species, *Coquillettidia (Coquillettidia) fuscopennata* (Theobald), *Coquillettidia (Coquillettidia) metallica* (Theobald), *Culex (Culex) annulioris* Theobald, *Coquillettidia (Coquillettidia) pseudoconopas* (Theobald), *Coquillettidia (Coquillettidia) aurites* (Theobald) and *Coquillettidia (Coquillettidia) maculipennis* (Theobald) were collected in relatively high abundance in the light traps (Table 1).

The most abundant species in human landing collections were *Ae. africanus* which comprised 65.9% of the total collections followed by *Cq. fuscopennata* (7.7%), *Cq. aurites* (7.5%) and *Aedes (Finlaya) ingrami* Edwards (5.2%). The most abundant species in ovitrap collections were *Ae. africanus* which comprised 76.8% of the total collections followed by *Culex (Culicomyia) cinereus* Theobald (11.8%) and *Aedes (Stegomyia) apicoargenteus* (Theobald) (5.1%). All the other species combined were less than 5% of the total ovitrap collections. Only three species were collected by all the three methods, namely; *Ae. africanus*, the *Culex (Culex) quinquefasciatus* Say and *Cx. cinereus* (Table 1). Of the 61 species collected, 21 were collected in both light traps and human-baited catches, but only one species, *Culex (Culex) moucheti* Evans, was collected in light traps and ovitraps (Table 1). Mosquitoes in the genera *Culex*, *Hodgesia* and *Mansonia* were frequently captured in human-baited catches and light trap collections however species in the genera *Mimomyia*

and *Uranotaenia* were only collected in light traps (Table 1). The *Aedes* species were collected in very low numbers in the light traps compared to human-bait and ovitrap methods. *Toxorhynchites* species were only collected in ovitraps (Table 1).

Aedes africanus was the most frequently captured species in human-baited catches and in ovitrap collections. The highest number of genera, species and number of mosquitoes were collected in light traps. The highest number of mosquitoes collected was in the genus *Coquillettia* and mostly in light traps collections (Fig. 2, 3 and 4), while the majority of the *Aedes* species were collected in human-baited catches and in ovitraps (Fig. 2). Overall, the most abundant mosquito species collected was *Cq. fuscopennata* which was 24% of the total collections followed by *Cq. metallica* (18%), *Cx. annulioris* (14%) and *Cq. pseudoconopas* (12%) (Table 1). *Coquillettia metallica* was the most frequently collected species from April through June 2010 (Fig. 5). In human-baited catches and ovitrap collections, the most frequently collected species were in the genus *Aedes* and the most abundant species in these collections was *Ae. africanus*, The *Aedes (Stegomyia) aegypti* group and *Toxorhynchites (Toxorhynchites) brevipalpis* Theobald were only collected in ovitraps (Fig. 2).

More mosquitoes were collected between January and May 2010 (Fig. 5) and there were significant differences between mosquitoes collected over the months (NPMANOVA, $p < 0.005$, $p = 0.0001$). The highest numbers of mosquitoes were collected at Sites 1 – 4 at ground level inside the forest and the least number of mosquitoes were collected at 30.5 m (100 ft) and 36.6 m (120 ft) stations on the tower. Relative humidity ($r = 0.065$, $P = 0.05$) and temperature ($r = 0.396$, $P = 0.05$) showed positive correlations with mosquito abundance which suggests that both humidity and temperature increased mosquito activity. On the other hand, rainfall had a significant negative effect ($r = -0.017$, $P = 0.05$) on the number of mosquitoes collected suggesting that thunderstorms inhibited mosquito activity.

Status of mosquito fauna before the 1970's compared with present

In Table 2 we summarize mosquito species that have previously been collected at Zika forest and the species we collected in 2010. Over 82 mosquito species were collected from Zika forest from 1955 to 1965 (Table 2). In the present study only 61 mosquito species were captured, but of these 24 were captured in Zika Forest for the first time, including: *Aedes (Aedimorphus) albocephalus* (Theobald), *Aedes (Aedimorphus) argenteopunctatus* (Theobald), *Aedes (Aedimorphus) marshallii* (Theobald), *Aedes (Neomelaniconion) luridus* McIntosh, *Aedes (Neomelaniconion) mcintonshi* Huang, *Aedes (Stegomyia) aegypti formosus* (Walker), *Aedes (Stegomyia) metallicus* (Edwards), *Culex (Culex) antennatus* (Becker), *Culex (Culex) neavei* Edwards, *Culex (Culex) perfuscus* Edwards, *Culex (Culex) pipiens* Linnaeus, *Cx. quiquefasciatus*, *Culex (Culex) vansomereni* Edwards, *Culex (Eumelanomyia) horridus* Edwards, *Culex (Eumelanomyia) kingianus* Edwards, *Culex (Oculeomyia) bitaeniorynchus* Giles, *Mimomyia (Mimomyia) hispida* (Theobald), *Mimomyia (Mimomyia) mimomyiaformis* (Newstead), *Mimomyia (Mimomyia) plumosa* (Theobald), *Mimomyia (Mimomyia) splendens* Theobald, *Mimomyia (Etorleptomyia) mediolineata* (Theobald), *Uranotaenia (Uranotaenia) connali* Edwards, *Uranotaenia (Pseudofilcobia) mashonaensis* Theobald, *Uranotaenia (Pseudofilcobia) nigromaculata* Edwards and *Uranotaenia (Pseudofilcobia) nivipous* Theobald were captured in Zika for the

first time (Table 2). However, 20 species previously reported for Zika Forest were not represented in our collections, including: *Anopheles (Anopheles) paludis* Theobald, *Coquillettia (Coquillettia) versicolor* (Edwards), *Culex (Eumelanomyia) fimbriforceps* Edwards, *Culex (Culex) guiarthi* Blanchard, *Culex (Culex) ingrami* Edwards, *Culex (Culicomyia) macfieii* Edwards, *Culex (Culicomyia) semibrunneus* Edwards, *Culex (Eumelanomyia) subrima* Edwards, *Mimomyia (Mimomyia) femorata* (Edwards), *Ficalbia circumtestacea* (Theobald), *Eretmapodites vansomereni* Hamon, *Eretmapodites oedipodeius* Graham, *Toxorhynchites (Toxorhynchites) kaimosi* (Van someren), *Aedes (Neomelanicion) taeniorostris* (Theobald), *Uranotaenia (Pseudoficalbia) fusca* Theobald, *Uranotaenia (Uranotaenia) pallidocephala* Theobald, *Aedes (mucidos) nigerimus* (Theobald), *Aedes (Aedimorphus) domesticus* (Theobald), *Eretmapodites quinquevittatus* Theobald, *Aedes (mucidos) grahamii* (Theobald) previous collected in Zika (Corbet 1961, Haddow et al. 1964, Haddow 1964, Haddow et al. 1968) (Table 2).

DISCUSSION

Our data shows variations in the species composition of Zika Forest from the last published species lists more than 40 years ago. Twenty-one of the 24 species collected in Zika Forest for the first time during our studies were captured using light traps (Tables 1 and 2). The primary collection method used in Zika Forest before the mid 1970s was human landing catches and this may have precluded these species from previous detection in Zika Forest. In addition, *Ae. luridus*, *Ae. marshallii*, *Cx. kingianus*, *Cx. bitaeniorynchus*, *Mi. splendens*, *Mi. plumosa* and *Mi. mediolineata* were each represented by less than 5 specimens in our collections (Table 1) suggesting that these species are extremely rare in Zika Forest or difficult to detect. However, some species especially in the genera *Mimomyia* and *Uranotaenia* were captured in relatively high abundance (Fig. 2) suggesting that these species are abundant in Zika Forest, but probably only readily collected in light traps. Three species detected for the first time in Zika Forest but captured by methods other than CO²-baited light traps included *Ae. aegypti formosus*. However, there is the possibility that the *Ae. aegypti aegypti* previously reported in Zika forest was *Ae. aegypti formosus* since the two species are morphologically very similar and all recent mosquito surveys have not detected *Ae. aegypti aegypti* in Uganda. The fact that 1% of *Cx. antennatus* were captured in human landing catches and the rest in CO² baited light traps suggested that this species may have previously been collected in Zika Forest but, there was a tendency of lumping together and processing *Culex* mosquitoes collected in human landing catches as *Culex* species and not identifying them to species (Haddow et al. 1964). *Aedes metallicus* was only captured in human landing catches (Table 1) but, only one specimen was collected in twelve months (Table 1) suggesting that this species is extremely rare in Zika Forest. It is possible that *Ae. metallicus* has been present in Zika Forest but in low densities and has been undetected until our studies in 2009 – 2010. Alternatively, *Ae. metallicus* may have been recently introduced to the areas by the human activity around Zika Forest. However, the fact that all 24 species have previously been captured in other regions of the country (Corbet 1961, Haddow 1945, 1946, 1948, 1954, Simpson et al. 1965, Haddow and Ssenkubuge 1965, 1974, Lutwama 2000) shows that all these species are native to Uganda and their recent detections in Zika forest do not represent new introductions to the country.

The 20 species that were previously collected in Zika by Corbet (1961), Haddow et al. (1964) and Haddow et al. (1968) (Table 2) and not detected in our collections may reflect variations in species composition or variations in relative abundance from year to year in Zika Forest, or localized extinction in Zika Forest during the last 40 years.

Of the 61 mosquito species we collected in Zika Forest, arboviruses of public health importance have previously been isolated from at least 31 (50.8%). The arboviruses associated with these species include; Chikungunya virus (Weinbren et al. 1958), Zika virus (Weinbren and Williams 1958), Rift Valley Fever virus (Haddow et al. 1964), O'nyong-Nyong virus (Rwaguma et al. 1997, Lanciotti et al. 1998, Kiwanuka et al. 1999, Lutwama et al. 1999, Sanders et al. 1999), Sindbis virus (Woodall 1964), Bunyamwera virus (Smithburn et al. 1946), Wesselsbron virus and Banzi virus (Henderson et al. 1968), Ntaya virus (Smithburn and Haddow 1951), Semliki Forest virus (Finter 1964), West Nile virus and Usutu virus (Smithburn et al. 1940, Williams et al. 1964), Witwatersrand virus and Germiston virus (Monath et al. 1972), and Uganda S virus (Dick and Haddow 1952). This suggests a high potential for transmission and maintenance of a wide range of arboviruses of public health importance within Zika Forest.

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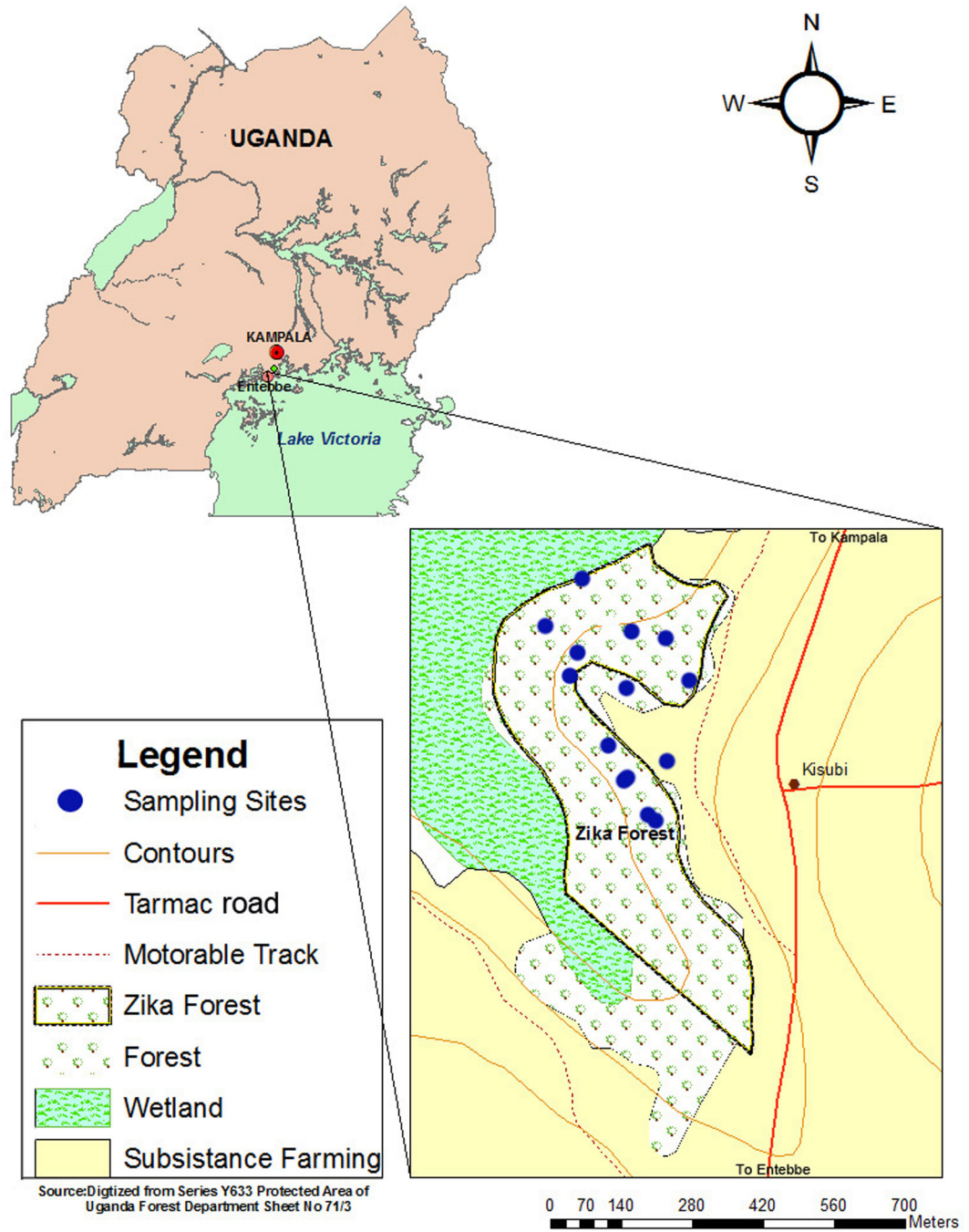


Fig. 1: Location of Zika forest (study area) in Entebbe, Uganda showing sampling sites.

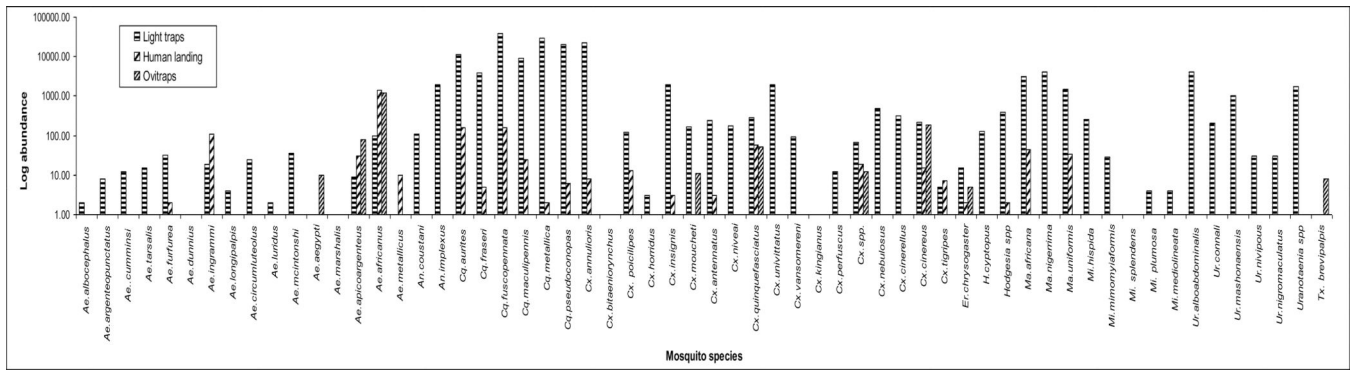


Fig 2: Abundance of mosquito species collected in Zika forest in 2009 and 2010. Oviposition trap, Human landing & Carbon dioxide-baited light trap collections.

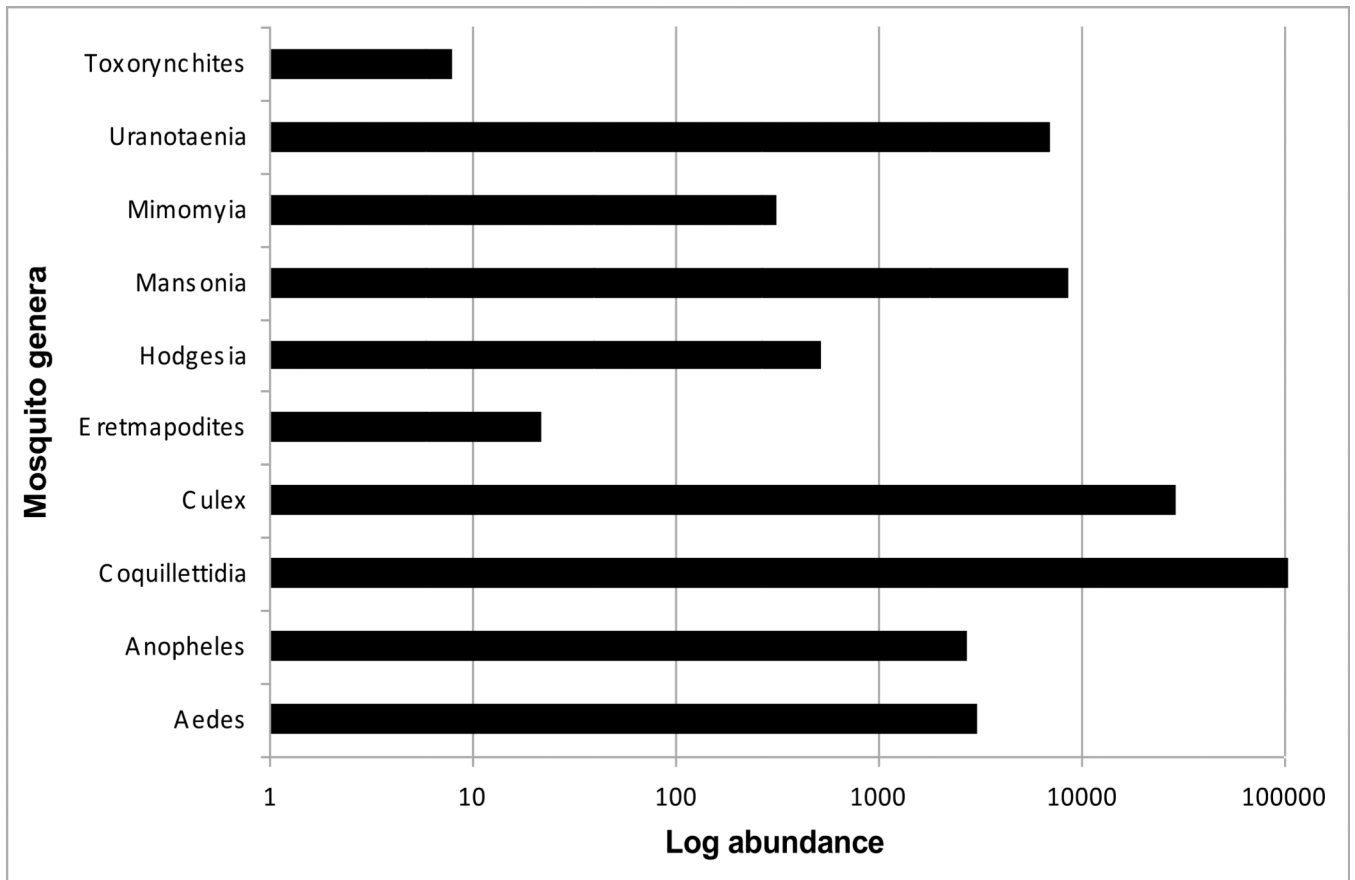


Fig. 3:
Mosquito genera collected in Zika forest in 2009 and 2010.

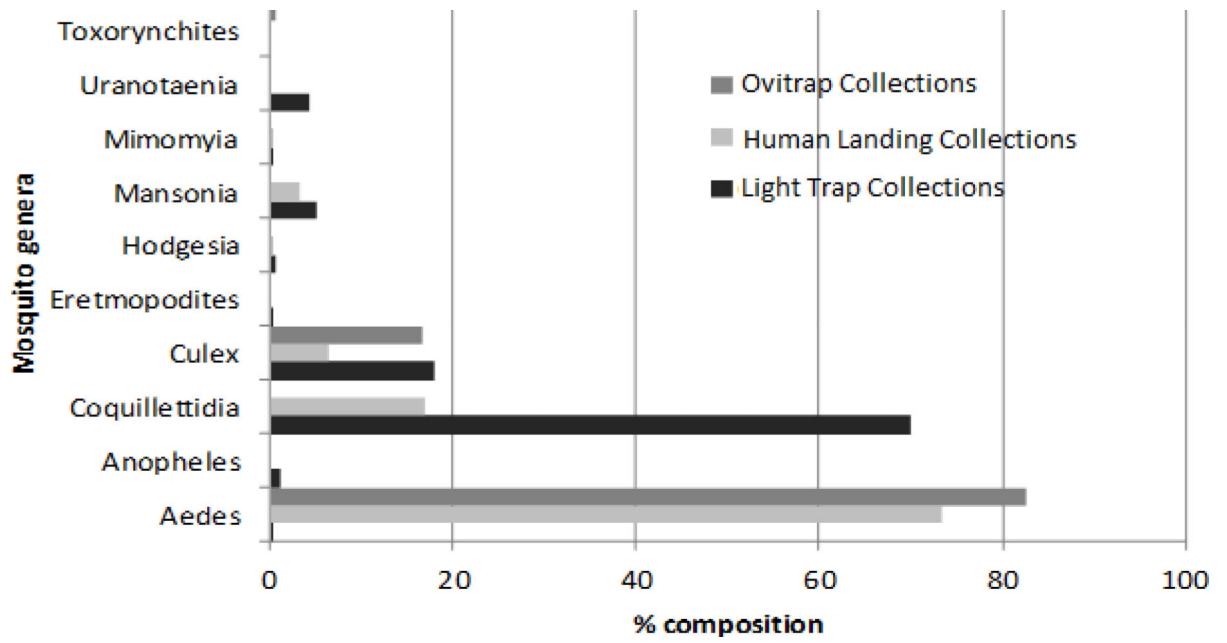


Fig. 4: Percentage composition of mosquito collections in the light trap, human landing and ovitrap collections in Zika forest, 2009–2010.

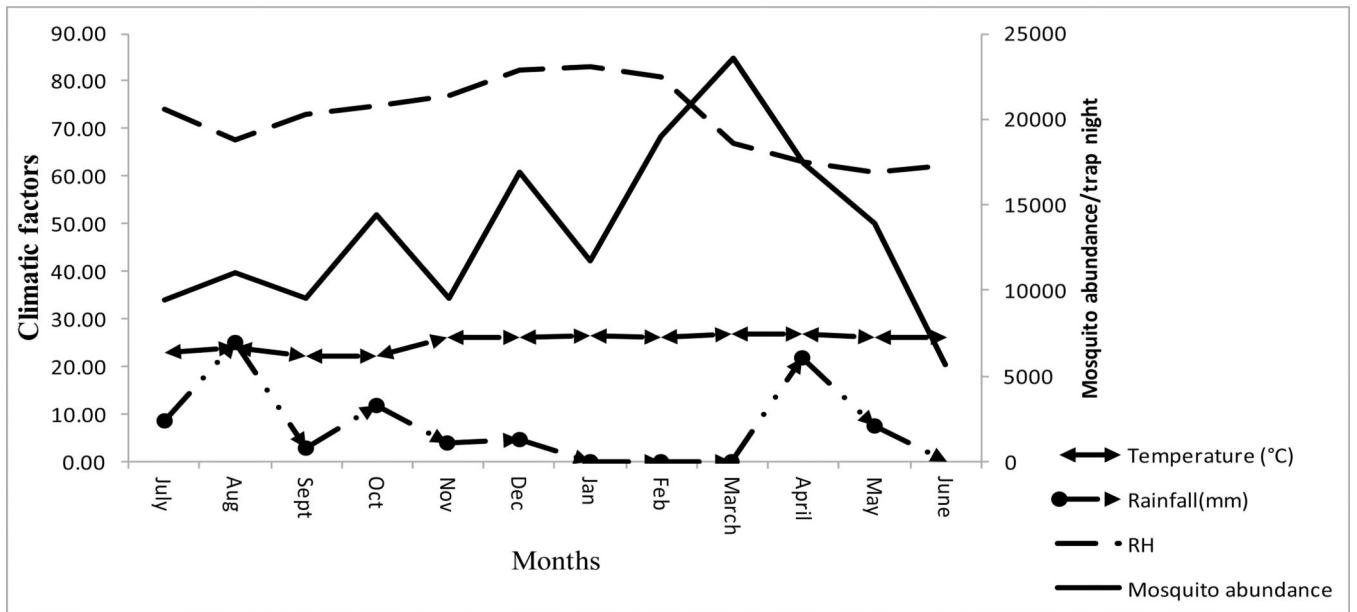


Fig 5:
Change in mosquito abundance with climatic parameters (temperature, rainfall and relative humidity) over the sampling period.

Mosquito species collected in Zika forest, Uganda, from July 2009 through August 2010 by using CO₂-baited light traps, human-baited catches and ovitraps.

Table 1.

Genus	Subgenus	Species	Light traps	Human	Ovitraps	Totals
<i>Aedes</i>	(<i>Aedinorphus</i>)	<i>albocephalus</i> (Theobald)	2	0	0	2
<i>Aedes</i>	(<i>Aedinorphus</i>)	<i>argenteopunctatus</i> (Theobald)	8	0	0	8
<i>Aedes</i>	(<i>Aedinorphus</i>)	<i>cumminsii</i> (Theobald)	12	0	0	12
<i>Aedes</i>	(<i>Aedinorphus</i>)	<i>marshali</i> (Theobald)	1	0	0	1
<i>Aedes</i>	(<i>Aedinorphus</i>)	<i>tarsalis</i> (Newstead)	15	0	0	15
<i>Aedes</i>	(<i>Aedionomyia</i>)	<i>fururea</i> (Enderlein)	32	1	0	33
<i>Aedes</i>	(<i>Dunnis</i>)	<i>spp</i>	1	0	0	1
<i>Aedes</i>	(<i>Finlaya</i>)	<i>ingrami</i> Edwards	19	108	0	127
<i>Aedes</i>	(<i>Finlaya</i>)	<i>longipalpis</i> (Gruenberg)	4	0	0	4
<i>Aedes</i>	(<i>Neomelanimonion</i>)	<i>circumluteolus</i> (Theobald)	25	0	0	25
<i>Aedes</i>	(<i>Neomelanimonion</i>)	<i>luridus</i> McIntosh	1	0	0	1
<i>Aedes</i>	(<i>Neomelanimonion</i>)	<i>mcintoshi</i> Huang	36	0	0	36
<i>Aedes</i>	(<i>Stegomyia</i>)	<i>aegypti formosus</i> (Walker)	0	0	10	10
<i>Aedes</i>	(<i>Stegomyia</i>)	<i>africanus</i> (Theobald)	98	1380	1199	2678
<i>Aedes</i>	(<i>Stegomyia</i>)	<i>apicourgenus</i> (Theobald)	9	0	79	88
<i>Aedes</i>	(<i>Stegomyia</i>)	<i>metallicus</i> (Edwards)	0	1	0	1
<i>Anopheles</i>	(<i>Anopheles</i>)	<i>coustani</i> Laveran	109	0	0	109
<i>Anopheles</i>	(<i>Anopheles</i>)	<i>inplexus</i> (Theobald)	1908	0	0	1908
<i>Coquillettidia</i>	(<i>Coquillettidia</i>)	<i>aurites</i> (Theobald)	11212	157	0	11369
<i>Coquillettidia</i>	(<i>Coquillettidia</i>)	<i>fraseri</i> (Theobald)	3970	5	0	3975
<i>Coquillettidia</i>	(<i>Coquillettidia</i>)	<i>fiscopennata</i> (Theobald)	38599	162	0	38761
<i>Coquillettidia</i>	(<i>Coquillettidia</i>)	<i>maculipennis</i> (Theobald)	9199	18	0	9217
<i>Coquillettidia</i>	(<i>Coquillettidia</i>)	<i>metallica</i> (Theobald)	29560	2	0	29562
<i>Coquillettidia</i>	(<i>Coquillettidia</i>)	<i>pseudocoenopax</i> (Theobald)	19710	7	0	19717
<i>Culex</i>	(<i>Culex</i>)	<i>antennatus</i> (Becker)	246	3	0	249
<i>Culex</i>	(<i>Culex</i>)	<i>neavei</i> Theobald	179	0	0	179
<i>Culex</i>	(<i>Culex</i>)	<i>perfuscus</i> Edwards	12	0	0	12

Genus	Subgenus	Species	Light traps	Human	Ovitrap	Totals
<i>Culex</i>	(<i>Culex</i>)	<i>pipiens</i> Linnaeus	280	58	53	391
<i>Culex</i>	(<i>Culex</i>)	<i>quinquefasciatus</i> Say	10	0	0	10
<i>Culex</i>	(<i>Culex</i>)	<i>univittatus</i> Theobald	1891	0	0	1891
<i>Culex</i>	(<i>Culex</i>)	<i>vansomeri</i> Edwards	93	0	0	93
<i>Culex</i>	(<i>Culex</i>)	spp.	46	20	12	78
<i>Culex</i>	(<i>Culicomyia</i>)	<i>cinerellus</i> Edwards	321	1	0	321
<i>Culex</i>	(<i>Culicomyia</i>)	<i>cinerus</i> Theobald	218	15	184	417
<i>Culex</i>	(<i>Culicomyia</i>)	<i>nebulosus</i> Theobald	497	0	0	497
<i>Culex</i>	(<i>Eumelanomyia</i>)	<i>horridus</i> Edwards	3	0	0	3
<i>Culex</i>	(<i>Eumelanomyia</i>)	<i>insignis</i> (Carter)	1922	3	0	1925
<i>Culex</i>	(<i>Eumelanomyia</i>)	<i>kingianus</i> Edwards	1	0	0	1
<i>Culex</i>	(<i>Kitzmillera</i>)	<i>moucheti</i> Evans	166	0	11	177
<i>Culex</i>	(<i>Lutzia</i>)	<i>tigris</i> De Grandpre & De Charmoy	5	7	0	12
<i>Culex</i>	(<i>Oculeomyia</i>)	<i>annulioris</i> (Edwards)	22974	8	0	22982
<i>Culex</i>	(<i>Oculeomyia</i>)	<i>bitaeniorynchus</i> Giles	1	0	0	1
<i>Culex</i>	(<i>Oculeomyia</i>)	<i>poecilipes</i> (Theobald)	121	10	0	131
<i>Culex</i>	(<i>Oculeomyia</i>)	<i>chrysogaster</i> Graham	15	0	5	20
<i>Eretmapodites</i>		<i>cyrtopus</i> Theobald	129	0	0	129
<i>Hodgesia</i>	(<i>Hodgesia</i>)	spp.	390	2	0	392
<i>Hodgesia</i>	(<i>Hodgesia</i>)	<i>africana</i> (Theobald)	3138	32	0	3170
<i>Mansonia</i>	(<i>Mansoniodes</i>)	<i>africana nigerrima</i> Theobald	4053	0	0	4053
<i>Mansonia</i>	(<i>Mansoniodes</i>)	<i>uniformis</i> (Theobald)	1510	33	0	1543
<i>Mimomyia</i>	(<i>Mimomyia</i>)	<i>hispidula</i> (Theobald)	252	0	0	252
<i>Mimomyia</i>	(<i>Mimomyia</i>)	<i>minomyiaformis</i> (Newstead)	28	0	0	28
<i>Mimomyia</i>	(<i>Mimomyia</i>)	<i>splendens</i> Theobald	1	0	0	1
<i>Mimomyia</i>	(<i>Mimomyia</i>)	<i>plumosa</i> (Theobald)	4	0	0	4
<i>Mimomyia</i>	(<i>Etoleptomyia</i>)	<i>mediolineata</i> (Theobald)	4	0	0	4
<i>Toxorhynchites</i>	(<i>Toxorhynchites</i>)	<i>brevipalpis</i> Theobald	0	0	8	8
<i>Uranotaenia</i>	(<i>Uranotaenia</i>)	<i>alboabdominalis</i> Theobald	4001	0	0	4001
<i>Uranotaenia</i>	(<i>Uranotaenia</i>)	<i>connali</i> Edwards	210	0	0	210
<i>Uranotaenia</i>	(<i>pseudofluctuata</i>)	<i>mashonensis</i> Theobald	1037	0	0	1037

Genus	Subgenus	Species	Light traps	Human	Ovitrap	Totals
<i>Uranotaenia</i>	(<i>pseudofilicabia</i>)	<i>nigromaculata</i> Edwards	30	0	0	30
<i>Uranotaenia</i>	(<i>pseudofilicabia</i>)	<i>nivipous</i> Theobald	30	0	0	30
<i>Uranotaenia</i>	(<i>Uranotaenia</i>)	spp.	1766	0	0	1766
Total			160,134	2,095	1,561	163,790

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Table 2.

Mosquito species collected in the present study, 2009–2010, compared to species collected in earlier years in Zika forest, Uganda.

Genus	Subgenus	Species	Period				
			1955–57	1960–61	1961–62	1964–65	2009–10
<i>Aedes</i>	<i>Aedimorphus</i>	<i>abnormalis</i> (Theobald) ^{a,c,f}	-	-	+	-	-
		<i>albocephalus</i> (Theobald)	-	-	-	-	+
		<i>argenteopunctatus</i> (Theobald)	-	-	-	-	+
		<i>cumminsii</i> (Theobald) ^{c,df}	-	+	-	-	+
		<i>domesticus</i> (Theobald) ^{a,c,f}	+	-	-	-	-
		<i>marshalii</i> (Theobald)	-	-	-	-	+
		<i>tarsalis</i> (Newstead) ^{c,f}	-	-	+	-	+
		<i>furpurea</i> (Enderlein) ^{c,f}	-	-	+	-	+
		<i>Dunnius</i> spp.	-	-	-	-	+
		<i>ingrami</i> Edwards ^{a,b, c, d, f, g, h}	+	+	+	+	+
<i>Finlaya</i>		<i>longipalpis</i> (Guenberg) ^{a,c,f,h}	+	-	+	-	+
		<i>nigerrimus</i> (Theobald) ^{a,c,f,g,h}	+	+	+	+	-
		<i>grahamii</i> (Theobald) ^{a,c,h}	+	+	+	-	-
<i>Mucidus</i>		<i>scatophagoideus</i> (Theobald) ^{c,f}	-	-	-	+	-
		<i>circumluteolus</i> (Theobald) ^{a,c,f,h}	+	-	+	-	+
		<i>luridus</i> McIntosh	-	-	-	-	+
		<i>mcintoshii</i> Huang	-	-	-	-	+
<i>Stegomyia</i>		<i>aegypti</i> (Walker)	-	-	-	-	+
		<i>africanus</i> (Theobald) ^{a,b,c,f,g,h}	+	+	+	+	+
		<i>apicoargenteus</i> (Theobald) ^{a,b,c,d,f,g,h}	+	+	+	+	+
<i>Anopheles</i>	<i>Anopheles</i>	<i>metallicus</i> (Edwards)	-	-	-	-	+
		<i>coustanti</i> Laveran	-	+	-	-	+
		<i>implexus</i> (Theobald) ^{a,b,c,f,h}	+	+	+	-	+

Genus	Subgenus	Species	Period					
			1955-57	1960-61	1961-62	1964-65	2009-10	
		<i>obscurus</i> (Granberg) ^{c,f}	-	-	+	-	-	
		<i>paludis</i> Theobald ^{a,b,c,d,f,g}	-	-	+	+	-	
	<i>Cellia</i>	<i>gambiae</i> Giles ^{a,c,f}	-	+	-	-	-	
		<i>marshallii</i> (Theobald) ^{c,f}	-	-	+	-	-	
		<i>moucheti</i> Evans, ^g	-	-	-	-	-	
		<i>wellcomei</i> Theobald ^c	-	-	+	-	-	
	<i>Coquillettidia</i>	<i>aurites</i> (Theobald) ^{a,b,c,d,f,g,h}	+	+	+	+	+	
		<i>fraseri</i> (Theobald) ^{a,b,c,d,f,g}	-	+	+	-	+	
		<i>fuscopennata</i> (Theobald) ^{a,b,c,d,f,g,h}	+	+	+	+	+	
		<i>maculipennis</i> (Theobald) ^{a,b,c,d,f,g,h}	+	+	+	+	+	
		<i>metallica</i> (Theobald) ^{a,b,c,d,f,g,h}	+	+	+	+	+	
		<i>pseudocoenopis</i> (Theobald) ^{a,b,c,d,f,g,h}	+	+	+	+	+	
		<i>antennatus</i> (Becker)	-	-	-	-	+	
	<i>Culex</i>	<i>guiarti</i> Blanchard ^{a,b,d,h}	+	-	-	-	-	
		<i>macfieii</i> Edwards ^{b,e}	-	-	-	+	-	
		<i>neavei</i> Edwards	-	-	-	-	+	
		<i>perfuscus</i> Edwards	-	-	-	-	+	
		<i>quiquestriatus</i> Say	-	-	-	-	+	
		<i>subrima</i> Edwards ^b	-	-	-	+	-	
		<i>univittatus</i> Theobald ^{a,b,g}	-	-	-	+	+	
		<i>vansomereni</i> Edwards	-	-	-	-	+	
	<i>Culicomyia</i>	<i>cinere/lus</i> Edwards ^f	-	-	+	+	+	
		<i>cinereus</i> Theobald ^{a,d,e}	-	-	+	+	+	
		<i>nebulosus</i> Theobald ^{a,b,g,h}	+	-	-	+	+	
	<i>Eumelanomyia</i>	<i>horridus</i> Edwards	-	-	-	-	+	

Genus	Subgenus	Species	Period					
			1955-57	1960-61	1961-62	1964-65	2009-10	
		<i>insignis</i> (Carter) ^{a,c,f,g}	-	+	+	+	+	
		<i>kingianus</i> Edwards ^a	-	-	-	-	+	
	<i>Kitzmilleria</i>	<i>moucheti</i> Evans ^{a,b,h}	+	-	-	-	+	
	<i>Lutzia</i>	<i>tigris</i> De Grandpre and De Charmoy ^h	+	-	-	-	+	
	<i>Oculeomyia</i>	<i>annulioris</i> (Edwards) ^{a,b,c,g,h}	+	+	+	+	+	
		<i>bitaeniorhynchus</i> Giles	-	-	-	-	+	
		<i>poecilipes</i> (Theobald) ^{c,f,g}	-	-	+	+	+	
<i>Eretmapodites</i>		<i>chrysoaster</i> Graham ^{a,b,c,d,f,h}	+	+	+	-	+	
		<i>oedipodeios</i> Graham ^{a,b,c,f,h}	+	+	+	-	-	
		<i>quinquevittatus</i> Theobald ^{a,c,f}	-	-	+	-	-	
<i>Filcabia</i>		<i>uniformis</i> (Theobald) ^h	+	-	-	-	-	
<i>Hodgesia</i>	<i>Hodgesia</i>	<i>cytopus</i> Theobald ^{a,b,c,d,f,g,h}	+	+	+	+	+	
<i>Malaya</i>		<i>taeniorostris</i> (Theobald) ^{a,b}	-	-	-	+	-	
<i>Mansonia</i>	<i>Mansonioides</i>	<i>africana africana</i> (Theobald) ^{a,b,c,d,f,g,h}	+	+	+	+	+	
		<i>africana nigerrima</i> Theobald ^{a,b,c,d,f,g,h}	-	-	-	-	+	
		<i>uniformis</i> (Theobald) ^{a,b,c,d,f,g,h}	+	+	+	+	+	
<i>Mimomyia</i>	<i>Mimomyia</i>	<i>hispidai</i> (Theobald) ^a	-	-	-	-	+	
		<i>mimomyiaformis</i> (Newstead)	-	-	-	-	+	
		<i>plumosa</i> (Theobald) ^a	-	-	-	-	+	
		<i>splendens</i> Theobald	-	-	-	-	+	
	<i>Etorleptomyia</i>	<i>mediolineata</i> (Theobald)	-	-	-	-	+	
<i>Toxorhynchites</i>	<i>Toxorhynchites</i>	<i>brevipalpis</i> Theobald	-	-	-	-	+	
<i>Uranotaenia</i>	<i>Uranotaenia</i>	<i>alboabdominalis</i> Theobald ^{b,d,h}	+	-	-	-	+	
		<i>caeruleocephala</i> Theobald ^h	+	-	-	-	-	

Genus	Subgenus	Species	Period				
			1955-57	1960-61	1961-62	1964-65	2009-10
		<i>connali</i> Edwards	-	-	-	-	+
		<i>pallidocephala</i> Theobald ^{b,d}	-	-	-	+	-
	<i>Pseudofitcobia</i>	<i>mashonaensis</i> Theobald	-	-	-	-	+
		<i>nigromaculata</i> Edwards ^d	-	-	-	-	+
		<i>nivipous</i> Theobald	-	-	-	-	+

^aWilliams 1964

^bGoma 1965

^cHaddow 1963 –1965

^dGoma et al. 1965

^eGoma 1964

^fHaddow and Ssenkubuge 1965

^gHaddow et al. 1968

^hHaddow 1964

Species without references were collected in Zika Forest for the first time in 2009-2010.