

Blood-feeding patterns of *Culex quinquefasciatus* and other culicines and implications for disease transmission in Mwea rice scheme, Kenya

Ephantus J. Muturi · Simon Muriu · Josephat Shililu ·
Joseph M. Mwangangi · Benjamin G. Jacob ·
Charles Mbogo · John Githure · Robert J. Novak

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Abstract Studies were conducted in Mwea Rice Scheme, Kenya during the period April 2005 and January 2007 to determine the host-feeding pattern of culicine mosquitoes. Mosquitoes were collected indoors and outdoors and tested for human, bovine, goat, and donkey blood meals by an Enzyme-Linked Immunosorbent Assay. A total of 1,714 blood-engorged samples comprising *Culex quinquefasciatus* Say (96.1%), *Culex annulioris* Theobald (1.8%), *Culex poicilipes* Theobald (0.9%), *Aedes cuminsi* Theobald (1.0%), *Aedes taylori* Edwards (0.1%), and *Mansonia africana* Theobald (0.1%) were tested. Except for *A. taylori*, in which the single blood meal tested was of bovine origin, the other species fed mostly on both bovine (range 73.3–100%) and goats (range 50–100%). Donkeys were also common hosts for all species (range 19.4–23.5%) except *A. taylori* and *M. africana*. *C. quinquefasciatus* was the only species containing human blood meals (0.04), and indoor collected populations of this species had significantly higher

frequency of human blood meals (9.8%) compared with outdoor-collected populations (3.0%). Mixed blood feeding was dominant among culicine species comprising 50.0%, 73.3%, 73.5%, 80.6%, and 94.1% of the samples for *M. africana*, *C. poicilipes*, *C. quinquefasciatus*, *C. annulioris*, and *A. cuminsi*, respectively. Ten mixed blood meal combinations including a mixture of all the four hosts were observed in *C. quinquefasciatus*, compared to one blood meal combination for *M. africana*, and two combinations for *C. poicilipes*, *C. annulioris*, and *A. cuminsi*. Mixed bovine and goat blood meal was the most common combination among the five culicine species followed by a mixture of donkey, bovine, and goat blood meals. We conclude that culicine species in Mwea are least likely to be vectors of lymphatic filariasis due to their high “preference” for livestock over human hosts, but they present an increased risk for arbovirus transmission particularly Rift Valley Fever virus, in which domestic animals serve as amplification hosts.

E. J. Muturi (✉) · B. G. Jacob · R. J. Novak
Department of Medicine,
William C. Gorgas Center for Geographic Medicine,
University of Alabama at Birmingham,
206C Bevell Biomedical Research Building,
845 19th Street South,
Birmingham, AL 35294, USA
e-mail: emuturi@uab.edu

S. Muriu · J. Shililu · J. M. Mwangangi · J. Githure
Human Health Division,
International Centre of Insect Physiology and Ecology,
Nairobi, Kenya

J. M. Mwangangi · C. Mbogo
Centre for Geographic Medicine Research-Coast,
Kenya Medical Research Institute,
Kilifi, Kenya

Introduction

The subfamily Culicinae is a diverse group of mosquitoes comprised of many genera that differ in both their biology and behavior. This group is also known to contain important vectors of lymphatic filariasis (LF) and several arboviruses notably Rift Valley Fever (RVF) virus, dengue fever, yellow fever, West Nile Virus (WNV), Japanese encephalitis, and many others (White 1989; Gubler 1996). In Africa, where one-third of the global burden of LF occurs, *Culex quinquefasciatus* Say is known to be one of the major vectors (Thompson et al. 1996; Mwandawiro et al. 1997; Bogh et al. 1998). In addition, several species of *Aedes* and *Culex* are known to transmit yellow fever,

RVF, and dengue viruses and have been involved in major outbreaks of these diseases in several African countries (Gubler 2004; Diallo et al. 2005; Rynn 2007). Understanding the potential risk of different culicine species in disease transmission and development of appropriate early warning systems and vector-control strategies is therefore urgently required in order to minimize the burden of culicine-borne diseases.

Blood-feeding patterns are considered one of the most important components of disease transmission. This information makes it possible to estimate the degree of human–vector contact and to understand the role of a given species in disease transmission cycle, both of which are critical for vector-control measures (Garret-Jones et al. 1980). Several factors including host preference, host availability, host density, and host irritability are known to influence blood feeding by mosquitoes (Washino and Tempelis 1983). These factors play a significant role in determining the epidemiological significance of a particular mosquito species. Species with a narrow host range such as *Anopheles gambiae* Giles s.s., *Anopheles funestus* Giles and *C. quinquefasciatus* are considered important vectors of both malaria and Bancroftian filariasis and those that switch between hosts are considered important in arbovirus transmission (Chandler et al. 1975b). Other studies have shown that diversion of host-seeking mosquitoes can reduce the risk of disease transmission (Burkot 1988; Reuben et al. 1992). In view of this concept, zoophylaxis is considered a potential tactic to control mosquito-borne diseases (Arunachalam et al. 2005; Mahande et al. 2007).

In rice-growing areas of the African continent, high populations of vector mosquitoes are known to co-exist (Chandler et al. 1975a; Snow 1983; Lacey and Lacey 1990; Muturi et al. 2006). Although this does not necessarily translate to increased malaria transmission (Ijumba and Lindsay 2001), existing evidence do indicate that rice cultivation increases the risk of lymphatic filariasis (Hunter 1992; Thompson et al. 1996; Appawu et al. 2001) as well as epidemic arbovirus transmission (Fontenille et al. 1998; Diallo et al. 2005). Surprisingly, most studies in irrigated areas focus mainly on malaria vectors at the expense of other mosquito species (Ijumba et al. 2002; Dolo et al. 2004). Therefore, substantial information is available on the blood-feeding patterns of malaria vectors in these areas (Chandler et al. 1975b; Ijumba et al. 2002; Dolo et al. 2004), but little is known about the feeding patterns of other mosquito species. A study in the rice-growing area of the Kano Plain, Kenya, reported that *Mimomyia mediolineata* Theobald and *Mimomyia splendens* Theobald fed mainly on amphibians and occasionally on man, while *Uranotaenia balfouri* Theobald and *Mimomyia hispida* Theobald fed mainly on amphibians and cattle (Boreham et al. 1975). Further studies in the same area found that *Coquillettidia karandalaensis* Wolfs, *Culex poecilipes* Theobald, and *Culex*

univittatus Theobald were highly ornithophilic species (Chandler et al. 1976) while *Mansonia uniformis* Theobald, *Mansonia africana* Theobald, *Culex antennatus* Becker, *C. univittatus*, *Aedes circumluteolus* Theobald, and *Aedes ochraceus* Theobald had preference for human and cattle hosts (Chandler et al. 1975b). Apart from these studies, knowledge on the feeding pattern of culicine mosquitoes in African rice agroecosystems is scanty. Because environmental factors are known to influence mosquito-feeding patterns (Washino and Tempelis 1983), it is often impossible to compute a general estimate of feeding patterns to be used throughout a species distribution range. The current study examined the blood-feeding pattern of six culicine species in Mwea Rice Irrigation Scheme in Central Kenya. This area was recently hit by a Rift Valley Fever virus epidemic (Centers for Disease Control 2007).

Materials and methods

Study area

The studies were conducted in Mwea Rice Irrigation Scheme in central Kenya, 100 km north-east of Nairobi. The study area has been described in detail by Mutero et al. 2004, Mwangangi et al. 2006, and Muturi et al. 2007. The Mwea Rice Irrigation Scheme covers an area of approximately 13,600 ha with forty villages and 150,000 people in 2,500 households. More than 75% of the land in each village is under rice cultivation with the remaining area being used for subsistence farming and human habitation. Four villages, Rurumi, Karima, Kiuria, and Kangichiri, were randomly selected for this study. Cattle, goats, and chickens are the main domestic animals found in all four study sites. Donkeys are also found in each of the sites but in low numbers. The majority of houses are mud-walled with iron roofing and unscreened eaves and windows. Seventeen known culicine species occur in the area with *C. quinquefasciatus* as the dominant species (Muturi et al. 2006). There is no data implicating any of the 17 culicine species with disease transmission in the area but they are considered potential vectors of arboviruses. The recent report of Rift Valley Fever virus cases in the area serves to confirm this claim (Centers for Disease Control 2007). *C. quinquefasciatus* is also considered a potential vector of Bancroftian filariasis together with *Amopheles arabiensis* (the main malaria vector in the area; Muturi et al. 2006, 2008).

Mosquito collection

Adult mosquito collections were conducted biweekly between April 2005 and January 2007. Indoor-resting

mosquitoes were collected using the pyrethrum spray catch (PSC) method (World Health Organization 1975) and outdoor populations were collected by Centers for Disease Control (CDC) miniature light traps (J.W. Hock Ltd, Gainesville, FL, USA). The mosquitoes in each study site were collected in twenty randomly selected houses (0700–1100 h) and six light trap stations (1800–0700 h). A detailed explanation of the sampling strategy has been described elsewhere (Muturi et al. 2006).

Laboratory processing

All culicine mosquitoes collected by PSC and CDC light traps were transported to the laboratory and sorted by sex and species using morphological characteristics as described by Edwards (1941). The females were further classified into their respective blood-feeding stages (unfed, blood-fed, semi-gravid, and gravid) by examining their abdomen under a dissecting microscope (World Health Organization 1975). All blood-fed mosquitoes from each collection were preserved in labeled vials containing anhydrous calcium sulphate (drierite).

Blood meal identification

Samples of blood-fed mosquitoes were cut transversely between the thorax and the abdomen using a sterile scalpel for each sample. The posterior portions containing the blood meal were placed individually in labeled vials. The abdomen of each mosquito was ground in 50 μ l of phosphate-buffered saline (PBS) with subsequent addition of 950 μ l of PBS and then stored at -20°C . Blood meals were identified by a direct enzyme-linked immunosorbent assay (ELISA) using anti-host (IgG) conjugates (Kirkegaard and Perry, Gaithersburg, MD) against human, bovine, donkey, and goat (Beier et al. 1988). All blood meal samples were first screened for human and bovine blood meals and later for goat and donkey blood meals. Positive controls included serum for each host tested, and different combinations human, bovine, goat, and donkey serum mixtures in PBS. Negative controls comprised ground male mosquitoes in PBS. This setup ensured that the samples were monitored for any possible cross reaction.

Statistical analyses

Data were analyzed using SPSS version 11.5 statistical package (SPSS, Inc., Chicago, IL). Because there was no significant site-to-site variation in mosquito-feeding pattern, the data for the four villages was pooled before analysis. Chi-square test was used to compare the difference in human blood index (HBI) between indoor and outdoor-collected *C. quinquefasciatus* mosquitoes.

Results

A total of 6,122 blood-fed mosquitoes were collected indoors and outdoors during the study period. These comprised *C. quinquefasciatus* (6,047), *C. annulioris* Theobald (36), *C. poicilipes* (17), *A. cuminsi* Theobald (17), *A. taylori* Edwards (two) and *M. africana* (three). From this total, 1,714 samples were tested for blood meal sources. These included 1,648 *C. quinquefasciatus*, 31 *C. annulioris*, 15 *C. poicilipes*, 17 *A. cuminsi*, one *A. taylori*, and two *M. africana*. The single blood meal specimen for *A. taylori* was of bovine origin, whereas one of the two specimens of *M. africana* was of bovine origin and the other was a mixture of bovine and goat. Blood meal sources for the other species were from at least three of the four hosts tested, with bovine and goats as the most common hosts (Table 1). All the four hosts were found to be sources of *C. quinquefasciatus* blood meals with proportions of 86.2%, 72.5%, 18.9%, and 3.9% for bovine, goats, donkeys, and human blood meals, respectively. The proportion of indoor collected *C. quinquefasciatus* containing human blood meals was 9.8% and significantly higher than 3.0% for outdoor-collected populations ($\chi^2=21.863$, $df=1$, $P<0.05$). The other species; *C. poicilipes*, *C. annulioris*, and *A. cuminsi* had taken their blood meals from all hosts except humans. The proportion of bovine, goat, and donkey blood meals, respectively, was 73.3%, 73.3%, and 13.3% for *C. poicilipes*, 90.3%, 80.6%, and 19.4% for *C. annulioris*, and 94.1%, 100%, and 23.5% for *A. cuminsi*. These species had taken their blood meals outdoors rather than indoors (Table 1). The positive controls for our ELISA analysis did not show any evidence of cross reaction.

With exceptions of *A. taylori*, in which the single blood meal sample was identified to be from a single host, and *M. africana*, where one of the two samples tested was a mixture of bovine and goat, the largest proportion of the blood meals for all of the other species were from more than one host. The percentage of mixed blood meals ranged from 73.3% (11 of 15) of the samples for *C. poicilipes* to 94.1% (16 of 17) of the samples for *A. cuminsi* (Table 2). Overall, only 26.2% of the blood meal samples were from a single host.

The various combinations of mixed blood meals obtained from different mosquito species are shown in Table 3. *C. quinquefasciatus* was found to have ten different combinations of mixed blood meals. The dominant mixed blood meal combination for this species was a mixture of goat and bovine (75.5%). Other common combinations were donkey, bovine, and goat mixtures (18.4), donkey and bovine mixtures (1.9%) and donkey and goat mixtures (1.5%). Five *C. quinquefasciatus* specimens had a mixture of all four hosts. Two blood meal

Table 1 Blood-feeding pattern of six culicine species in Mwea Rice Scheme, Kenya

Species	Location	# Tested	Human (%)	Cow (%)	Donkey (%)	Goat (%)
<i>C. quinquefasciatus</i>	Indoors	204	20 (9.8)	108 (52.9)	52 (25.5)	90 (44.1)
	Outdoors	1444	44 (3.0)	1312 (90.9)	260 (18.0)	1104 (76.5)
	Overall	1648	64 (3.9)	1420 (86.2)	312 (18.9)	1194 (72.5)
<i>C. poicilipes</i>	Indoors	5	0 (0.0)	3 (60.0)	0 (0.0)	3 (60.0)
	Outdoors	10	0 (0.0)	8 (80.0)	2 (20.0)	8 (80.0)
	Overall	15	0 (0.0)	11 (73.3)	2 (13.3)	11 (73.3)
<i>C. annulioris</i>	Indoors	8	0 (0.0)	5 (62.5)	1 (12.5)	5 (62.5)
	Outdoors	23	0 (0.0)	23 (100)	5 (21.7)	20 (87.0)
	Overall	31	0 (0.0)	28 (90.3)	6 (19.4)	25 (80.6)
<i>A. cuminsi</i>	Indoors	1	0 (0.0)	1 (100.0)	0 (0.0)	1 (100.0)
	Outdoors	16	0 (0.0)	15 (93.8)	4 (25.0)	16 (100.0)
	Overall	17	0 (0.0)	16 (94.1)	4 (23.5)	17 (100.0)
<i>A. taylori</i>	Indoors	0	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
	Outdoors	1	0 (0.0)	1 (100.0)	0 (0.0)	0 (0.0)
	Overall	1	0 (0.0)	1 (100.0)	0 (0.0)	0 (0.0)
<i>M. Africana</i>	Indoors	0	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
	Outdoors	2	0(0.0)	2 (100.0)	0 (0.0)	1 (50.5)
	Overall	2	0(0.0)	2 (100.0)	0 (0.0)	1 (50.5)
Total		1714	64 (3.7)	1478 (86.2)	324 (18.9)	1248 (72.8)

combinations; bovine and goat mixtures and donkey, bovine and goat mixtures were found in *C. poicilipes* and *C. annulioris*. Bovine and goat was the dominant combination for both species accounting for 81.8% and 76.0% of mixed blood meals for *C. poicilipes* and *C. annulioris*, respectively. *A. cuminsi* had two mixed blood meal combinations; bovine and goat mixtures (75%), and donkey, bovine, and goat mixtures (25.0%).

Discussion

Our study demonstrated the highly zoophilic nature of culicine mosquitoes collected at the Mwea, Kenya study sites. With the exception of *C. quinquefasciatus*, which fed on humans at low frequency, the other species fed on livestock, mainly on cattle and goats and less frequently on

donkeys. Bogh et al. (1998) reported a human blood index (HBI) of 0.9 for indoor collected *C. quinquefasciatus* along the Kenyan coast. In western Kenya, the HBI for indoor and outdoor-collected *C. quinquefasciatus* was 0.88 and 0.23, respectively (Beier et al. 1990). Our HBI results for this species were 0.10 and 0.03, respectively for indoor and outdoor-collected populations, and therefore many times lower than in the western or coastal regions of Kenya. We did not conduct a census of domestic animals, but a quick observation revealed that cattle and goats were more common than donkeys and therefore more likely to be encountered by host-seeking mosquitoes. Chicken, dogs, cats, wild birds, and rodents were also present but lack of resources could not allow us test them as sources of mosquito blood meals. These animals are known to be important sources of blood meals for mosquitoes in the area (Kamau et al. 2003) and should be included in future studies. Importantly, we neither found any negative samples in our blood meal analysis nor evidence for cross reaction. However, it is possible that many blood meals were a mixture of identified and unidentified hosts. Moreover, out of the 17 culicine species known to occur in the area, blood-fed samples were only obtained for six species and all except one species had very few representatives. We are therefore cautious in interpretation of these results and recommend the need for further studies to establish the blood-feeding behavior of the diverse culicine species occurring in similar areas and their potential in disease transmission.

C. quinquefasciatus and *A. arabiensis* Patton are known to occur in higher densities in the study area compared with

Table 2 Proportion of different culicine species that had taken their blood meals from single or multiple hosts in Mwea Rice Scheme, Kenya

Species	Single host	Multiple hosts	Total
<i>Culex quinquefasciatus</i>	436 (26.5)	1,212 (73.5)	1,648
<i>Culex poicilipes</i>	4 (26.7)	11 (73.3)	15
<i>Culex annulioris</i>	6 (19.4)	25 (80.6)	31
<i>Aedes cuminsi</i>	1 (5.9)	16 (94.1)	17
<i>Aedes taylori</i>	1 (100.0)	0 (0.0)	1
<i>Mansonia africana</i>	1 (50.0)	1 (50.0)	2
Total	449 (26.2)	1,265 (73.8)	1,714

Table 3 Mixed blood meal combinations among culicine mosquitoes in Mwea Rice Scheme, Kenya

Blood meal combinations	<i>C. quinquefasciatus</i>	<i>C. poicilipes</i>	<i>C. annulioris</i>	<i>A. cuminsi</i>	<i>M. africana</i>
Bovine, goat	914 (75.5)	9 (81.8)	19 (76.0)	12 (75)	1 (100.0)
Donkey, goat	18 (1.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Human, bovine	6 (0.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Human, donkey	9 (0.7)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Donkey, bovine	23 (1.9)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Donkey, bovine, goat	223 (18.4)	2 (18.2)	6 (24.0)	4 (25.0)	0 (0.0)
Human, bovine, goat	12 (1.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Human, donkey, goat	1 (0.1)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Human, donkey, bovine	1 (0.1)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
All four hosts	5 (0.4)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Total	1212 (100.0)	11 (100.0)	25 (100.0)	16 (100.0)	1 (100.0)

adjacent non-irrigated areas (Muturi et al. 2006). Because of the greater biting nuisance associated with these vectors, most people in irrigated areas sleep under bed nets and use other mosquito-control tactics that force mosquitoes to seek alternative hosts (Ijumba and Lindsay 2001; Ijumba et al. 2002; Mutero et al. 2004). This may partly account for significantly lower HBI for culicine mosquitoes in the study area as compared with the non-irrigated areas of western or coastal Kenya. However, although the HBI for indoor collected *C. quinquefasciatus* was significantly higher than that of outdoor-collected population, it is difficult to tell whether a human blood meal was taken indoors or outdoors. Our data suggested that most individuals of this species entered the house after feeding outdoors on domestic animals. It is therefore likely that some or possibly all of the indoor collected mosquitoes had obtained human blood meals outdoors.

The low anthropophily observed for culicine mosquitoes in the present study could be both beneficial and detrimental to disease transmission. On the positive side, it may disfavor transmission of Bancroftian filariasis by *C. quinquefasciatus* through loss of significant number of worms to the wrong host, or by failing to pick up enough parasites that can sustain transmission. Generally, filariasis transmission is very inefficient because there is no parasite multiplication in the mosquito and continuous exposure to many infective bites is required (Bockarie et al. 2002). It has been estimated that as many as 15,500 infective bites by *C. quinquefasciatus* are required to produce a patent human infection (Hairston and De Meillon 1968). Such infective bites are unlikely to be obtained when the human-biting rates are low. The commonness of cattle and goat feeding by mosquito species in the current study may also reduce transmission of arboviruses that may require amplification in other domestic animals or in wild animals or birds. For instance, pigs play an important role in pre-epizootic amplification of Japanese encephalitis (JE) virus in southeast Asian countries that experience JE epidemics (Peiris et al. 1992) while cattle are

considered dead-end hosts (Ilkal et al. 1988). Japanese encephalitis prevalence is therefore high in areas where the pig population is higher relative to that of cattle (Colless 1959; Pennington and Phelps 1968; Mitchell et al. 1973) and low in areas where the cattle populations outnumber that of pigs (Reuben et al. 1992). Marsupials also have been reported to divert host-seeking mosquitoes away from pigs thereby impeding establishment of JE virus (van den Hurk et al. 2003). On the negative, these mosquito species presents a high risk of Rift Valley Fever (RVF) virus transmission. This virus is transmitted by *Aedes* species to domestic animals including cattle, goats, sheep, and camels where virus amplification occurs leading to propagation into various *Culex* species that spread the virus (McIntosh 1972). The feeding pattern for the species in Mwea therefore present an ideal condition for RVF, and efforts should be made to establish the risk factors of the disease in similar areas and to develop sustainable mosquito surveillance and control systems.

Our findings demonstrated that nearly all the species examined fed on multiple hosts within a single gonotrophic cycle. *C. quinquefasciatus* had the greatest number of mixed blood meal combinations and was the only species containing mixed blood meals from all of the four hosts tested. Mixed feeding within the same gonotrophic cycle is common among mosquitoes and its epidemiological significance has been greatly debated (Garret-Jones et al. 1980; Burkot 1988). Arunachalam et al. (2005) suggested that multiple feeding may favor or disfavor disease transmission depending on whether the vector feeds on potential hosts or dead-end hosts. For instance, cattle feeding by malaria vectors may reduce malaria transmission through loss of certain number of sporozoites in non-human hosts (Hadis et al. 1997). Like wise, multiple feeding of JE vectors on dead-end hosts such as cattle and goat may divert mosquitoes from potential hosts such as pigs and birds resulting in reduced JE transmission (Arunachalam et al. 2005). In contrast, multiple feeding on potential hosts such

as cattle and goats, as observed in our study, may enhance amplification and transmission of RVF. These findings illustrate that domestic animals can be both the cause of an increase in the disease and the avenue through which it could be reduced. It is therefore essential to understand how domestic animals may impact on different mosquito-borne diseases before adopting zooprophyllaxis as a disease-control strategy in similar areas.

In conclusion, our study has demonstrated the “preference” of domestic animals over humans by six culicine species. The study has shown that these mosquitoes have a tendency to feed on multiple hosts within the same gonotrophic cycle. Our findings demonstrate the great potential of these species to transmit RVF virus in similar areas. We recommend the need for sustained surveillance and control of these species in order to minimize the risk. More importantly, the potential role of domestic animals in arbovirus epidemiology should be evaluated before incorporating zooprophyllaxis as part of mosquito-borne disease-control tactic.

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