

LARVAL HABITAT DYNAMICS AND DIVERSITY OF *CULEX* MOSQUITOES IN RICE AGRO-ECOSYSTEM IN MWEA, KENYA

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Abstract. Introduction of irrigation projects in developing nations has often been blamed for aggravating the problem of mosquito-borne diseases by creating ideal larval habitats for vector mosquitoes. However, whereas several studies have demonstrated the relationship between malaria vectors and irrigation, little work has been done on culicine mosquitoes despite their potential in transmission of filariasis and arboviruses and their significant biting nuisance in these areas. This study examined the diversity of *Culex* mosquito fauna and their larval habitats at two sites (Murinduko and Kiamachiri) in Mwea, Kenya over a 12-month period. The habitat types present at each site within a 200-meter radius around the study village, including randomly selected paddies and canals, were sampled every two weeks to examine the relationship between vegetation cover, water depth, turbidity, and *Culex* larval counts. Ten culicine species belonging to four genera were identified, with 73.1% of the total collection comprising of *Culex duttoni* and *Cx. quinquefasciatus*. Other species collected included *Cx. annulioris*, *Cx. poicilipes*, *Cx. cinereus*, *Cx. tigripes*, *Cx. trifilatus*, *Aedes spp.*, *Coquilettidia fuscopennata*, and *Ficalbia splendens*. Murinduko was more diverse than Kiamachiri in terms of species richness (10 versus 7 species) and larval habitat diversity (11 versus 8 habitat types). Paddies, canals, and rain pools were the most diverse habitats in terms of species richness, and ditches, rock pools, and tree holes were the least diverse. Principal component and correlation analyses showed a strong association between three *Culex* species and the measured habitat characteristics. *Culex poicilipes* was strongly associated with floating vegetation, *Cx. annulioris* with clean water containing emergent vegetation, and *Cx. quinquefasciatus* was associated with turbid water. Seasonal changes in larval counts in water reservoirs and pool and ditch habitats were closely associated with rainfall. These findings provide important information on larval habitat preference for different *Culex* species, which will be useful in designing and implementation of larval control operations.

INTRODUCTION

In Africa, the population growth outpaces agricultural production.¹ In an effort to improve food security, water development projects have been developed, and many more continue to be developed. It is estimated that by the year 2020, 16 million hectares will be under irrigation.² This transformation is expected to alter the pattern of mosquito-borne diseases. Already, studies across Africa have demonstrated the negative impact of water development projects on mosquito borne diseases. Although introduction of irrigated agriculture has little or no impact on malaria transmission in areas of stable transmission,^{3,4} irrigated rice cultivation in semi-arid savannah zone of Africa can alter malaria transmission pattern from seasonal to perennial.^{5,6} An increase in the density of *Anopheles gambiae s.l.*, *An. funestus*, and *Culex quinquefasciatus* and a consequent increase in the prevalence of Bancroftian filariasis has also been reported after introduction of irrigated agriculture.^{7–9} Along the Senegal River Basin, *Cx. poicilipes* was incriminated as a new vector of Rift Valley Fever virus (RVFV) and was inferred to have been involved in 1998–1999 RVF outbreaks in the area.¹⁰ A survey of RVFV in the Turkwel Gorge Hydroelectric Project along the Kenya-Uganda border reported an isolate of West Nile virus from a pool of four male *Cx. univittatus*.¹¹ Collectively, these studies demonstrate the increasing burden of mosquito-borne diseases as a consequence of water agro-development projects and illustrate the need for closer collaborative links be-

tween water and health ministries to address the problem of mosquito-related diseases in these areas.

Among irrigated crops, rice is considered to pose the greatest danger to health because it is grown under flooded conditions. Studies in various parts of Africa have demonstrated that irrigated rice agro-ecosystems can support between 10 and 35 mosquito species,^{12–15} making them important targets for vector control operations. However, despite the distribution and abundance of diverse mosquito species in these areas, most research efforts have been directed towards *An. gambiae s.l.* and *An. funestus*.^{5,16–18} Consequently, little is known about the ecology of other rice land mosquitoes in spite of their epidemiologic significance. For instance, other than rice fields and associated habitats,^{19,20} it is unknown how other habitat types such as rain pools, stream pools, rock pools, tree holes, hoof prints, and marshes contribute to adult mosquito production in African rice agro-ecosystems. These non-paddy habitats are known to support a broad spectrum of mosquito species and should be targets for larval control interventions. For example, in Orissa, India, 13 mosquito species belonging to the genera *Aedes*, *Culex*, *Ochlerotatus*, *Orthopodomyia*, *Toxorhynchites*, *Tripteroides*, and *Uranotaenia* were collected in tree holes, 12 species from the genera *Anopheles*, *Aedes*, and *Culex* in ground pools, but only a single species, *An. jeyporiensis*, was found in paddy fields.²¹ Other important larval habitats observed in this study were bamboo, leaf axils, fallen logs, ponds, rock pools, and streams, which collectively accounted for 11 mosquito genera. Similar studies in Africa, Asia, and South America have demonstrated the important contribution of non-paddy habitats in production of diverse mosquito species.^{22–26} However, although several mosquito species may coexist in these aquatic habitats, evidence of differential habitat use has been documented.^{12,23}

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To address the problem of mosquito-borne diseases through larval control interventions in these areas, different propositions have been made. Fillinger and others²³ suggested the need to consider all potential larval habitats for larval control interventions, and Gu and Novak²⁷ argued for the need to identify all potential larval habitats and then direct larval control efforts to the most productive habitats. Although these studies differ in their final approach towards achieving effective larval control interventions, they accentuate the need for proper identification of all aquatic habitats in which mosquitoes thrive as a guide for vector control operations. The principal objective of this study was therefore to identify the diversity of larval habitats in which *Culex* mosquitoes flourish in two villages with different farming practices in Mwea, Kenya, and to quantify the contribution of each habitat type to mosquito productivity.

MATERIALS AND METHODS

Study area. The study was conducted in the Mwea Rice Irrigation Scheme in central Kenya, approximately 100 km northeast of Nairobi. The study area has been previously described.¹⁸ Mwea rice scheme occupies the lower altitude zone of Kirinyaga District in an expansive low-lying area characterized by black cotton soil. The annual rainfall varies from a maximum of 1,626 mm to a minimum of 356 mm, with an average of 950 mm per year. The average temperature is 21.3°C (range = 16.0–26.5°C) and the average relative humidity is 59.5% (range = 52–67%). According to the 1999 national census, Mwea division has an estimated population of 150,000 persons in 25,000 households. The Mwea Irrigation Scheme is located in the west central region of Mwea Division and covers an area of approximately 13,640 hectares. More than 50% of the scheme area is used for irrigated rice cultivation, and the remaining area is used for subsistence farming, grazing, and community activities. The species of the genus *Culex* that have been reported as adults in the study area include *Cx. quinquefasciatus*, *Cx. pocilipes*, *Cx. annulioris*, and *Cx. tigripes*.¹⁴ The presence of potential vectors of Bancroftian filariasis and arboviruses in the area makes it an important target for vector control studies.

Two villages, Kiamachiri and Murinduko, were selected for the study based on rice cultivation practices and the extent of rice coverage within a radius of 1 km from the village perimeter. Both villages are outside the Mwea rice irrigation scheme and differ in their agricultural practices. Kiamachiri is a rice-growing village with approximately 20% of the land under rice and is located approximately 2 km outside the scheme. The remaining 80% of the area is used for growing mainly maize, beans, and bananas. Murinduko is situated approximately 15 km from the scheme and is generally a non-rice-growing village because of its hilly topography that renders much of the area (approximately 90%) unsuitable for rice cultivation except for limited rice growing activity (less than 5% of the total area) along one major river valley that runs along the edge of the village. The soil in this area is highly porous and seepage of rain water is high. Maize, beans and bananas are the main crops cultivated but only on a subsistence scale in an area approximately 70% of the village.

Meteorologic data. A rain gauge (Tru-Chek®; Rain Gauge Division, Edwards Manufacturing Co., Albert Lea, MN) was

installed in each village and rainfall data was recorded daily over a period of 12 months (April 2004–March 2005). Temperature and relative humidity for each village was also taken using temperature and relative humidity data loggers (Onset Computer Corporation, Bourne, MA). BoxCar Pro (Onset Computer Corporation) was used to download weather information at the end of every month.

Larval sampling and processing. All non-paddy larval habitats present within each village were identified, categorized, and sampled every two weeks for mosquito larvae over a 12-month period (April 2004–March 2005). Five randomly selected paddy blocks 60 m × 60 m were also included and formed the sampling unit for the paddy habitat category. Diverse larval habitat types present in each paddy block were identified and sampled separately for mosquito larvae. Up to 20 dips were taken at intervals along the edge of each larval habitat using a standard mosquito dipper (350 mL) depending on the size of the aquatic habitat. For vegetated habitats, the vegetation was carefully opened up to allow for water pooling before dipping was done. The larvae for each habitat were placed separately in whirl paks and transported to the laboratory where they were sorted by genus and instar, counted, and recorded. All third and fourth instar culicine larvae were preserved in 100% ethanol and later identified morphologically to species.²⁸ Physical characteristics of the larval habitats, including water depth, turbidity, presence of floating and emergent vegetation, and the proportion of the aquatic habitat covered by floating vegetation, were recorded. Water depth was measured using a metal ruler, and the proportion of the aquatic habitat covered by floating vegetation was estimated visually. Turbidity that was mainly caused by suspended organic matter was measured through visual examination of the water against a white background and categorized as either clear or turbid.

Data analyses. Data analyses was performed using SPSS version 11.5 for Windows (SPSS Inc., Chicago, IL) and SYSTAT version 11 (SYSTAT Software Inc, San Jose, CA) statistical software. Variation in larval counts between villages was compared by Student *t*-test, and differences in larval counts among habitat types and months were analyzed using one-way analysis of variance (ANOVA). Where significant differences were observed in ANOVA, the Tukey test was used to separate the means. Variation in diversity of habitat types between villages was compared using the chi-square test. Pearson correlation analysis was used to assess the relationship between rainfall and larval counts in different habitat types and villages. Principle component analysis was used to separate the larval habitats based on the measured physical characteristics. The association between the derived factor scores and larval counts was determined by Pearson correlation analysis. Larval counts were expressed as the number of larvae per 20 dips because the number of larvae sampled was low. Statistical analyses was done using log transformed ($\log_{10} n + 1$) larval counts to normalize the data. Results were considered significant at $P < 0.05$.

RESULTS

Meteorology. The total precipitation for the period April 2004 to March 2005 was 764.4 mm. The rainfall pattern was bimodal, concentrated in April–May and September–December. In this period, the average daily temperature was 22.86°C

(range = 20.1–25.5°C) and the average relative humidity was 71.02% (range = 56.6–83.4%).

Larval abundance and habitat diversity. A total of 21,366 and 8,907 early and late instar culicine larvae, respectively, were collected in Murinduko and Kiamachiri during the 12-month study period. The relative abundance of early and late instars, respectively, was three-fold ($t = 9.73$, degrees of freedom [df] = 1, $P < 0.01$) and seven-fold ($t = 8.76$, df = 1, $P < 0.01$) higher in Murinduko than in Kiamachiri. The relative importance of different habitat types with regard to larval presence and productivity is shown in Table 1. Eleven habitat types were identified in Murinduko compared with eight habitat types in Kiamachiri ($\chi^2 = 608.005$, df = 11, $P < 0.01$). Of 1,735 samples that were collected in Kiamachiri during the 12-month period, 43% were positive for culicine larvae compared with 66.8% of the 1,778 samples in Murinduko. Paddy, canal, and pit habitats constituted most of the samples in Kiamachiri, and paddy, rain pool, stream pool, and canal habitats constituted most of the samples in Murinduko. Results of ANOVA and Tukey's honestly significantly differences tests showed that counts of late instars of culicine larvae in Kiamachiri were significantly higher in water reservoirs, ditches, seepage areas, and marshes compared with the other habitat types ($F = 4.087$, df = 7, $P < 0.01$). Similar analyses in Murinduko observed significantly higher larval counts in water reservoirs, rock pools, rain pools, and hoof prints than in the other habitat types ($F = 6.529$, df = 10, $P < 0.01$). However, in relation to long-term contribution to larval productivity, paddies, canals, and pits were more important because they had water available for culicine larval development when most of the other habitats were dry. They were therefore sampled more times for mosquito larvae compared with the other habitat types (Table 1).

The importance of each of these habitats in larval production was dependent upon the month and the village. Although some habitats were important in one village in a particular month ($F = 6.483$, df = 11, $P < 0.01$), they were either absent or less important in relation to other habitats in the other

village (Table 2). In Kiamachiri, paddies supported larval development throughout the 12-month period but in significantly higher numbers in September and October and between December and March ($F = 2.726$, df = 11, $P < 0.01$). Canals were also important habitats during most of the sampling period, with greater activity in October, November, and February ($F = 3.057$, df = 11, $P < 0.05$). The importance of marshes, seepage areas, and pits in larval productivity was not variable among seasons but in contrast, ditches, rain pools, and water reservoirs were productive mainly during the wet season (Table 2). In Murinduko, canals, paddies, marshes, seepage areas, stream pools, and rain pools supported larval development throughout most of the 12-month sampling period, and tree holes, water reservoirs, rock pools, ditches, and hoof prints were important at specific months. The most productive months for paddy habitats were January and February and June to August ($F = 7.115$, df = 11, $P < 0.01$) during which time the monthly rainfall was lowest ($r = -0.590$, df = 24, $P < 0.05$), and larval counts in canals, seepage areas, marshes, and rain and stream pools did not vary significantly among season. Larval development in tree holes occurred in December only while the importance of ditches, water reservoirs, and rock pools at specific months was closely associated with rainfall pattern (Table 2).

Species composition and abundance of culicine larvae. Some 68.5% ($n = 6,102$) of the total late stage culicine larvae collected were examined microscopically for species identification. The genus *Culex* ($n = 5,163$) was represented by seven species mainly dominated by *Cx. duttoni* (49.7%) and *Cx. quinquefasciatus* (36.6%). Other *Culex* species included *Cx. tigripes* (5.4%), *Cx. annulioris* (3.7%), *Cx. cinereus* (3.6%), *Cx. poecilipes* (0.9%), and *Cx. trifilatus* (0.1%). Two specimens each of *Coquillettidia fuscopennata* and *Ficalbia splendens* were also observed. The remaining specimens ($n = 935$) were indeterminate species of the genus *Aedes*. All species were represented in Murinduko, whereas *Cx. cinereus*, *Cx. trifilatus*, and *Fl. splendens* were not represented in Kiamachiri (Table 3). Overall, *Cx. duttoni* and *Cx. quin-*

TABLE 1

Relative abundance of culicine larvae collected from different habitat types and the proportion of aquatic habitats positive for culicine larvae in the two villages in Mwea, Kenya

Village	Habitat type	No. of habitats	No. of samples taken	Percent positive for Culex larvae	Counts of early instars/20 dips	Counts of late instars/20 dips	
Kiamachiri	Paddy	108	753	41.2	4.9	0.9	
	Canal	30	332	38.6	5.1	0.5	
	Ditch	8	24	50.0	27.6	3.4	
	Marsh	27	106	57.5	6.8	2.3	
	Pit	6	275	42.5	7.4	1.9	
	Seep	8	90	71.1	18.1	2.7	
	Water reservoirs	2	24	54.2	5.1	5.2	
	Pool	59	131	31.3	1.2	0.5	
	Total/mean	248	1,735	43.0	6.2	1.2	
	Murinduko	Paddy	83	1,127	64.1	14.0	6.9
		Canal	9	132	65.9	11.8	4.7
Ditch		5	13	76.9	10.8	1.7	
Hoof print		7	37	81.1	21.4	29.7	
Marsh		22	90	68.9	11.8	4.4	
Rock pool		4	14	78.6	55.9	33.3	
Seep		7	68	73.5	19.5	5.4	
Stream pool		10	107	67.3	12.4	3.9	
Water reservoirs		4	22	86.4	55.6	41.0	
Tree hole		3	3	100.0	11.0	0.0	
Pool		35	165	73.5	20.3	15.6	
Total/means		189	1,778	66.8	15.4	8.2	

TABLE 2

Seasonal contribution of different habitat types to culicine larval production (all stages) over the 12-month sampling period in the two villages in Mwea, Kenya*

Village	Month	No. of larvae per 20 dips												
		Rainfall (mm)	Paddy	Canal	Ditch	Hoof print	Marsh	Rock pool	Seep	Stream pool	Water reservoir	Tree hole	Pool	Pit
Murinduko	April 2004	119	1.0	0.0	3.0	5.3	2.0	22.5	2.3	10.1	8.5	0.0	14.9	–
	May 2004	56	3.1	0.8	4.0	0.0	1.9	9.7	14.1	3.4	4.0	0.0	2.0	–
	June 2004	10	33.5	15.0	0.0	16.0	13.1	10.0	18.0	14.8	0.0	0.0	26.2	–
	July 2004	0	40.2	28.8	8.0	28.0	46.9	32.0	14.7	11.0	0.0	0.0	20.0	–
	August 2004	9	37.6	32.6	0.0	191.0	16.0	0.0	36.4	16.3	0.0	0.0	29.0	–
	September 2004	15	13.6	16.3	19.0	43.3	7.3	0.0	78.3	31.3	0.0	0.0	34.1	–
	October 2004	190	9.9	14.7	24.0	26.0	10.4	22.0	3.6	9.2	142.0	0.0	29.3	–
	November 2004	324	7.7	2.8	19.5	16.0	20.0	499.0	8.0	5.0	67.7	0.0	141.0	–
	December 2004	54	15.0	10.4	14.0	10.0	13.0	56.5	11.3	6.8	74.3	11.0	10.8	–
	January 2005	6	27.4	19.1	0.0	31.3	15.0	0.0	22.5	5.4	276.0	0.0	17.7	–
	February 2005	4	26.3	8.2	0.0	0.0	31.6	0.0	16.0	14.7	105.0	0.0	10.4	–
	March 2005	23	15.6	13.3	0.0	0.0	33.3	0.0	62.7	51.1	72.0	0.0	19.4	–
	Total/mean	810.0	19.2	13.5	7.6	30.6	17.5	54.3	24.0	14.9	62.5	0.9	29.5	–
	Kiamachiri	April 2004	181.8	1.5	1.5	4.0	–	3.5	–	10.0	–	4.7	–	0.9
May 2004		74.8	1.6	0.5	1.1	–	1.6	–	5.6	–	0.4	–	1.6	11.9
June 2004		28	2.1	3.7	0.0	–	7.3	–	11.0	–	0.0	–	4.0	17.8
July 2004		8	6.5	4.1	400.0	–	7.7	–	7.8	–	0.0	–	2.0	7.2
August 2004		1.6	5.9	2.1	0.0	–	6.0	–	27.0	–	0.0	–	0.0	11.6
September 2004		71	11.3	0.8	0.0	–	2.7	–	5.7	–	0.0	–	0.0	5.9
October 2004		96.2	8.9	7.9	0.0	–	24.6	–	39.0	–	67.3	–	0.9	10.2
November 2004		136	4.4	9.3	123.3	–	16.6	–	30.0	–	3.5	–	2.2	11.7
December 2004		47.5	11.0	4.7	18.0	–	10.0	–	49.4	–	6.7	–	2.6	7.0
January 2005		21	10.1	2.3	6.0	–	25.7	–	9.1	–	26.0	–	4.4	4.6
February 2005		1	10.3	28.2	0.0	–	7.6	–	37.3	–	3.0	–	0.5	14.5
March 2005		13	10.1	2.1	0.0	–	0.0	–	0.0	–	0.0	–	0.0	9.4
Total/mean		679.9	7.0	5.6	46.0	–	9.4	–	19.3	–	9.3	–	1.6	9.7

* – indicates that no aquatic habitat was present.

quefasciatus accounted for 73.1% of the total mosquitoes identified and were represented in all habitat types except the tree holes. *Culex duttoni* occurred overwhelmingly in Murinduko and *Cx. quinquefasciatus* occurred abundantly in both villages. *Aedes spp.* was also represented in all habitat types except ditches and tree holes, and other species were

more restricted in their larval habitats with paddies, canals, pools, and pits supporting a wide range of species. In tree holes, only early instars of the sub-family Culicinae were found.

The monthly variation in the numbers of *Cx. quinquefasciatus* and *Cx. duttoni* in the two villages is shown in Figure 1.

TABLE 3

Distribution of culicine larvae in different larval habitats in the two villages in Mwea, Kenya*

Village	Habitat type	Paddy	Canal	Ditch	Hoof print	Marsh	Rock pool	Seep	Stream pool	Tank	Pool	Pit
Murinduko	<i>Aedes spp.</i>	288	43	0	113	26	39	29	38	64	194	–
	<i>Culex annulioris</i>	45	44	0	0	2	0	3	43	0	25	–
	<i>Cx. cinereus</i>	64	0	0	0	0	0	0	0	0	123	–
	<i>Cx. duttoni</i>	1,733	196	3	103	60	44	27	17	19	330	–
	<i>Cx. poicilipes</i>	18	1	1	0	0	0	0	0	7	6	–
	<i>Cx. quinquefasciatus</i>	832	154	8	21	50	81	79	37	8	110	–
	<i>Cx. tigripes</i>	126	19	2	10	8	0	10	6	4	39	–
	<i>Cx. trifilatus</i>	1	2	0	0	0	0	0	0	0	0	–
	<i>Coquilletidia</i>	1	0	0	0	0	0	0	0	0	0	–
	<i>Ficalbia splendens</i>	2	0	0	0	0	0	0	0	0	0	–
	Total	3,110	459	14	247	146	164	148	141	102	827	–
	Kiamachiri	<i>Aedes spp.</i>	51	12	0	–	10	–	3	–	0	4
<i>Cx. annulioris</i>		8	0	0	–	0	–	1	–	0	3	18
<i>Cx. cinereus</i>		0	0	0	–	0	–	0	–	0	0	0
<i>Cx. duttoni</i>		25	1	0	–	1	–	0	–	0	0	7
<i>Cx. poicilipes</i>		9	1	0	–	0	–	0	–	5	0	1
<i>Cx. quinquefasciatus</i>		180	68	14	–	63	–	69	–	7	17	91
<i>Cx. trigripes</i>		20	8	0	–	1	–	4	–	0	4	16
<i>Cx. trifilatus</i>		0	0	0	–	0	–	0	–	0	0	0
<i>Coquilletidia fuscopennata</i>		0	0	0	–	0	–	1	–	0	0	0
<i>Ficalbia splendens</i>		0	0	0	–	0	–	0	–	0	0	0
Total		293	90	14	–	75	–	78	–	12	28	154

* – indicates that no aquatic habitat was present.

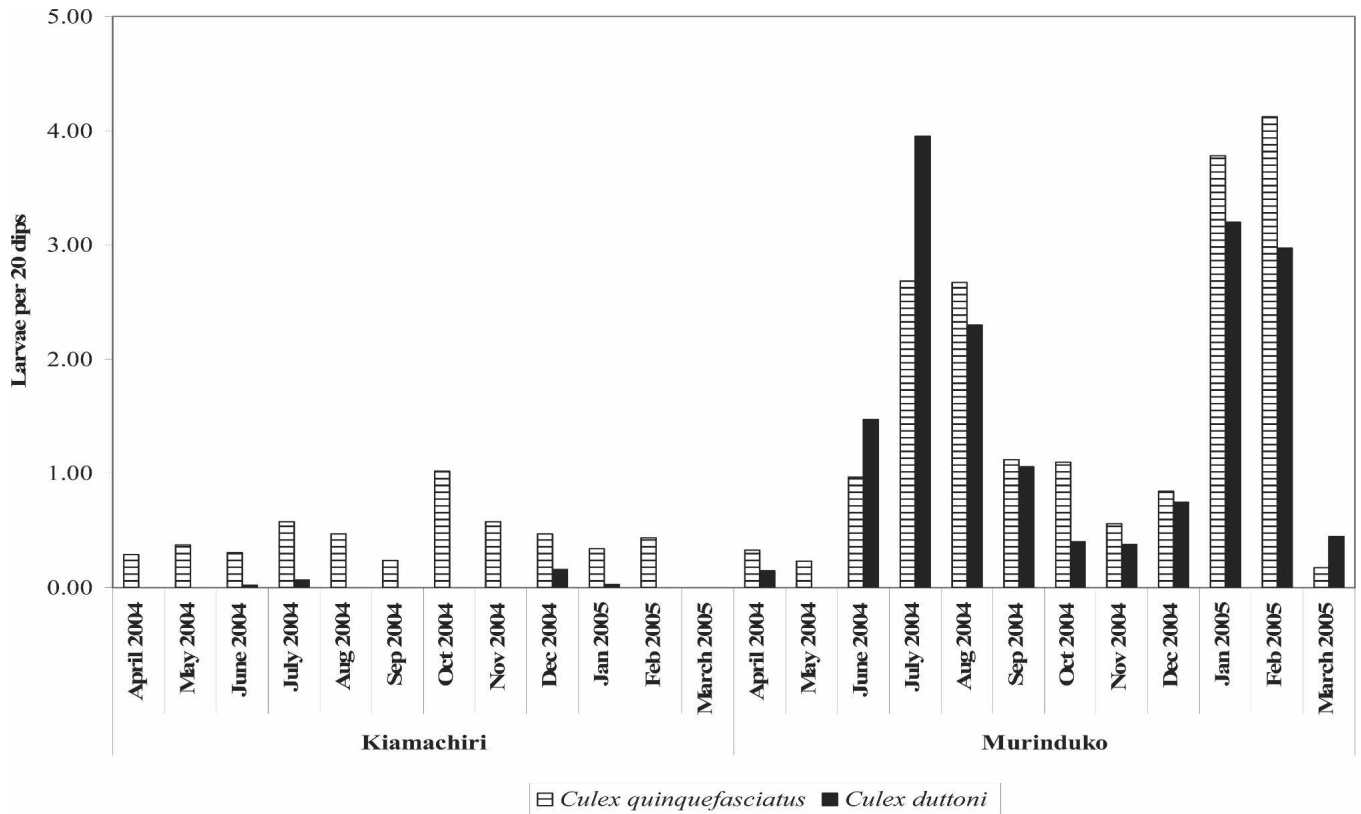


FIGURE 1. Monthly variation in the numbers of *Culex quinquefasciatus* and *Culex duttoni* in Kiamachiri and Murinduko villages, Mwea, Kenya.

In Kiamachiri, the numbers of *Cx. quinquefasciatus* were low throughout the sampling period with little variation among months. However, in Murinduko, the monthly variation in the numbers of *Cx. quinquefasciatus* and *Cx. duttoni* was evident. Two population peaks for both species were observed, the first in July–August 2004 and the second in January–February 2005.

Habitat characteristics and larval development. Three principle components explained 83.7% and 70.7% of the total variance based on the five environmental variables measured in Kiamachiri and Murinduko, respectively (Table 4). The first principle component (PC) was a linear combination of high loads on the floating vegetation cover (*Azolla*) and other types of floating vegetation describing a strong gradient of floating vegetation cover. The second PC was a linear combination with high loads on emergent vegetation on the positive side in Murinduko and on the negative side in Kia-

machiri. This separated habitats with emergent vegetation from those without. The third PC separated habitats with clean water from those with turbid water.

Results of the correlation analysis between culicine larval counts and habitat factors (or principal components) are shown in Table 5. A significant association between the three principle components and three *Culex* species was observed. *Culex poicilipes* was positively associated with PC 1 in Kiamachiri, which indicated a strong association with floating vegetation. *Culex annulioris* was negatively associated with PC 1 and positively associated with PC 2 in Kiamachiri and negatively associated with PC 3 in Murinduko. This means that *Cx. annulioris* larvae were positively associated with emergent vegetation and negatively associated with floating vegetation in Kiamachiri whereas in Murinduko, they were likely to be found in habitats with clean water. *Cx. quinquefasciatus* was positively associated with turbid water (PC 3).

TABLE 4
Principle component analysis of habitat variables and interpretation of derived principle components*

	Kiamachiri			Murinduko		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
% of the habitat covered by floating vegetation	0.862	0.319	0.153	0.8	-0.059	0.014
Emergent vegetation	0.360	-0.689	0.432	-0.009	0.875	0.104
Floating vegetation	0.867	0.315	0.139	0.793	-0.188	-0.084
Turbidity	0.383	-0.052	-0.863	-0.044	-0.211	0.966
Depth (cm)	-0.366	0.344	0.210	0.444	0.440	0.222
% variation explained	38.1	25.3	20.4	29.5	20.9	20.0

* PC 1 = a continuum for floating vegetation cover; PC 2 = a continuum for emergent vegetation; PC 3 = a continuum for turbidity; - indicates the direction of change with increasing principle component.

TABLE 5
Results of Pearson correlation analysis between mosquito densities and derived principle components*

Species	Kiamachiri			Murinduko		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
<i>Culex quinquefasciatus</i>	-0.007	0.020	0.041	-0.025	-0.024	0.060†
<i>Cx. poicilipes</i>	0.062†	-0.001	0.020	-0.025	0.012	-0.041
<i>Cx. annulirois</i>	-0.071†	0.060†	0.020	-0.017	-0.012	-0.067†
<i>Cx. duttoni</i>	-0.028	0.021	0.018	0.115	0.203	-0.004
<i>Aedes spp.</i>	-0.028	0.041	0.024	-0.047	-0.010	0.001
n	1,221	1,221	1,221	1,082	1,082	1,082

* PC 1 = a continuum for floating vegetation cover; PC 2 = a continuum for emergent vegetation; PC 3 = a continuum for turbidity; - indicates the direction of change with increasing principle component.

† Correlation is significant at 0.05 level (two-tailed).

The other culicine species were not significantly associated with any of the three principle components.

DISCUSSION

This study has documented the occurrence of seven species of the genus *Culex* in the study area. However, we were unable to document the species of *Culex* associated with tree holes because only early instars were represented in these habitats, which made it difficult to identify them morphologically to species. Our attempt to rear them to third instar in the laboratory to facilitate their morphologic identification was unsuccessful. Additionally, because of logistic difficulties, we did not sample other potential habitats such as leaf axils and fallen logs, which are also known to be ideal breeding grounds for some *Culex* species.²¹ Additional *Culex* species could be detected by further adult sampling and larval surveys.

The occurrence of diverse species of genus *Culex*, including important vectors of Bancroftian filariasis and arboviruses,^{7,29} represent a trade off between human health and the benefits accrued to irrigated rice cultivation. Thus, although rice growing is a key source of employment and income generation, urgent consideration must be given to reducing the density of the diverse mosquito species thriving in these areas if these benefits are to be realized. This is especially important in Africa where the surface area under irrigation currently estimated at only 8.5% is expected to increase significantly within the next few decades.³⁰

The diversity of habitat types had a marked effect on *Culex* species diversity. Murinduko, which had significantly more diverse habitat types, had a rich *Culex* mosquito fauna than Kiamachiri with fewer habitat types. Previous findings have reported a close association between larval habitats diversity and mosquito fauna.^{31,32} The results further demonstrated the possibility of targeting specific habitats at different times of the year depending on the season and site. Some habitats with the highest larval counts such as water reservoirs, ditches, pools, and hoof prints were mainly important during the wet season, and low-count habitats such as paddies and canals were productive throughout the study period. These findings are in agreement with previous observations that the most productive habitats per surface area are not necessarily the most important habitats for vector proliferation over space and time.²³ In Venezuela, Grillet²⁵ noted that a large number of low density, but continuously productive habitats contribute more to the adult mosquito density than singly high-density larval habitats. Importantly, the current study dem-

onstrated a significant negative association between rainfall and *Culex* larval densities in Murinduko where there was limited rice cultivation. In areas of intense rice cultivation, the rice cropping cycle is considered to impact significantly on mosquito production,³³ and rainfall is considered to be of insignificant short-term importance.³⁴ Conversely, in areas of little or no irrigation such as Murinduko, larval production is dependent upon temporary larval development sites.³¹ As rains begin, some time must elapse for water bodies to form to facilitate effective larval breeding.³⁴ Considering that most of the non paddy habitats in Murinduko were concentrated on stream edges and that the soils and topography of this village could not allow the formation of numerous rain-fed pools, it is logical to assume that productive habitats were rendered less productive after the rains because of flushing out of the larvae, as observed by previous investigators.^{35,36} From the public health point of view, these results indicate that a wide spectrum of *Culex* species thrive in a variety of habitat types whose larval densities vary with space and time depending on the underlying environmental and ecologic conditions. As such, any successful larval control operation, especially one targeting integrated control of diverse mosquito species occurring in a given area, should take into account the spatial-temporal dynamics in larval habitats productivity.

A preliminary study to determine the adult mosquito species diversity in the two studies sites during the same study period observed a higher density of *Culex* mosquitoes in Kiamachiri compared with Murinduko.¹⁴ Interestingly however, the current study observed the opposite trend in larval counts. However, these findings should be interpreted with caution. It should be noted that the two villages had different agricultural practices. In Kiamachiri, rice fields covered approximately 20% of the village and we only sampled a small fraction of these paddies. Thus, many more paddy habitats were contributing to adult populations than were sampled. In contrast, Murinduko was mainly a non-irrigated village with only less than 5% of the land under rice cultivation. More than 70% of the paddy habitats in this village were sampled for mosquito larvae in addition to all the other aquatic habitats within the 200-meter radius. Therefore, most larval habitats were sampled in Murinduko compared with only a few representatives in Kiamachiri, and this may account in part for the differences in larval counts between the two villages. This demonstrates one of the complications encountered in larval sampling when trying to compare the differences in mosquito densities among areas with different amount of land modified by agricultural practices.

Culex duttoni and *Cx. quinquefasciatus* occurred widely in diverse habitat types, but other species were restricted to a few habitat types. This may explain why they were the predominant species. Principle component analysis did not show any significant association between *Cx. duttoni* and any of the five parameters that were measured in this study, which is probably an indication of its ability to thrive in a variety of ecologic conditions as reported by Hopkins.²⁸ *Culex quinquefasciatus* was abundant in habitats with turbid water, *Cx. poicilipes* in habitats with floating vegetation, and *Cx. annulioris* was mainly associated with clean water in which emergent vegetation was present. In most areas of its distribution, *Cx. quinquefasciatus* prefer habitats with turbid water caused by organic matter,^{19,37} as was the case in the present study. Little is known about the breeding of *Cx. annulioris*, and *Cx. poicilipes* in Africa but records from Edwards³⁸ and Berner³⁹ reported *Cx. annulioris* to prefer clean water containing filamentous algae, an analog of floating vegetation in our study, and *Cx. poicilipes* was found in clean vegetated habitats. This study illustrates that larval production is a function of complex interaction of several biotic and abiotic habitat characteristics,^{25,32} many of which were not measured in this study. Moreover, this study was more descriptive than comprehensive. A more quantitative study is warranted, which would include physical, chemical, and biologic habitat characteristics and their impact not only on species diversity but on abundance and seasonal periodicity.

This study provides baseline information on *Culex* mosquitoes at two sites targeted for malaria vector control by microbial larvicides. The results have demonstrated a wide spectrum of *Culex* mosquitoes in relation to rice cultivation. The study suggests that rice cultivation has a marked effect on *Culex* mosquito species diversity. It also illustrates the importance of how human-made changes could alter species diversity and abundance. The results reaffirm the need to consider peridomestic and natural habitats present in a given area, if significant reduction in mosquito densities is to be realized through larval management. These findings also provide significant information useful in designation of an integrated mosquito control strategy in response to the recent emergence and re-emergence of mosquito-borne diseases in the tropics. An integrated vector control program is advantageous because in addition to reducing the risk of mosquito-borne diseases, it could also result in an overall reduction in densities of nuisance mosquitoes making it more acceptable to the surrounding community.

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