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Author(s): Ephantus J. Muturi, Joseph Mwangangi, Josephat Shililu, Benjamin G. Jacob, Charles Mbogo, John Githure, and Robert J. Novak

Source: Journal of Vector Ecology, 33(1):56-63. 2008.

Published By: Society for Vector Ecology

DOI: [http://dx.doi.org/10.3376/1081-1710\(2008\)33\[56:EFAWTD\]2.0.CO;2](http://dx.doi.org/10.3376/1081-1710(2008)33[56:EFAWTD]2.0.CO;2)

URL: <http://www.bioone.org/doi/full/10.3376/1081-1710%282008%2933%5B56%3AEFAWTD%5D2.0.CO%3B2>

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Environmental factors associated with the distribution of *Anopheles arabiensis* and *Culex quinquefasciatus* in a rice agro-ecosystem in Mwea, Kenya

Ephantus J. Muturi¹✉, Joseph Mwangangi^{2,4}, Josephat Shililu^{2,3}, Benjamin G. Jacob¹, Charles Mbogo⁴, John Githure², and Robert J. Novak¹

¹Department of Medicine, William C. Gorgas Center for Geographic Medicine, 206C Bevell Biomedical Research Building, 845 19th Street South, University of Alabama at Birmingham, Birmingham, AL 35294, U.S.A.

²Human Health Division, International Centre of Insect Physiology and Ecology, Nairobi, Kenya

³Department of Zoology, Jomo Kenyatta University of Agriculture and Technology, Nairobi, Kenya

⁴Centre for Geographic Medicine Research-Coast, Kenya Medical Research Institute, Kilifi, Kenya

Received 6 July 2007; Accepted 3 December 2007

ABSTRACT: Studies were conducted between May and June, 2006 to investigate the environmental factors affecting the distribution of *An. arabiensis* Patton and *Culex quinquefasciatus* Say in Mwea, Kenya. The sampling unit comprised all non-paddy aquatic habitats and ten randomly selected paddies and canals located within a 200 m radius from the periphery of the study site. Thirteen physico-chemical variables were recorded for each sampling site in each sampling occasion and a sample of mosquito larvae and other aquatic invertebrates collected. The non-paddy aquatic habitats identified included pools and marshes. Morphological identification of 1,974 mosquito larvae yielded four species dominated by *Cx. quinquefasciatus* (73.2%) and *An. arabiensis* (25.0%). Pools were associated with significantly higher *Cx. quinquefasciatus* larval abundance and less diversity of other aquatic invertebrates compared with other habitat types. In contrast, the abundance of *An. arabiensis* did not differ significantly among habitat types. *Culex quinquefasciatus* habitats had higher water conductivity and exhibited a higher abundance of other aquatic invertebrates than *An. arabiensis* habitats. Chi-square analysis indicated that the two species were more likely to coexist in the same habitats than would be expected by chance alone. *Anopheles arabiensis* larvae were positively associated with dissolved oxygen and adults of family Haliplidae and negatively associated with emergent vegetation and Heptageniidae larvae. *Culex quinquefasciatus* larvae were positively associated with dissolved oxygen, total dissolved solids, Chironomidae larvae, and Microvelidae adults and negatively associated with emergent vegetation. These findings suggest that both biotic and abiotic factors play a significant role in niche partitioning among *Cx. quinquefasciatus* and *An. arabiensis*, a factor that should be considered when designing an integrated vector control program. **Journal of Vector Ecology 33 (1): 56-63. 2008.**

Keyword Index: *An. arabiensis*, *Cx. quinquefasciatus*, environmental factors, integrated vector management, rice agro-ecosystem, Kenya.

INTRODUCTION

Mosquito species differ in the type of aquatic habitats they prefer for oviposition based on location, the physico-chemical condition of the water body, and the presence of potential predators (Shililu et al. 2003, Piyaratnea et al. 2005). Physico-chemical factors that influence oviposition, survival, and the spatio-temporal distribution of important disease vector species include salts, dissolved organic and inorganic matter, degree of eutrophication, turbidity, presence of suspended mud, presence or absence of plants, temperature, light and shade, and hydrogen ion concentration (Mogi 1978, Amerasinghe et al. 1995, Gimnig et al. 2001). Understanding how these factors affect the distribution of a particular vector species and how they influence larval abundance is an essential component of larval biology and of great importance in the design and implementation of integrated vector management plans.

Several studies have examined the relationship between habitat characteristics and larval abundance. In Sri Lanka,

Anopheles culicifacies Giles was positively associated with light and vegetation and negatively associated with the presence of potential predators, while *Anopheles varuna* Iyengar was positively associated with a variety of aquatic fauna (Piyaratnea et al. 2005). In Venezuela, salinity and dissolved oxygen were associated with the spatial distribution of *Anopheles aquasalis* Curry and *Anopheles oswaldoi* Peryassu (Grillet 2000). In Orange County, CA, U.S.A., the distribution of *Culex tarsalis* Coquillett was significantly associated with the percent cover by *Typha* spp. root masses and *Typha* spp. stem density per square meter (Walton et al. 1990). *Culex quinquefasciatus* Say larvae, in Peninsular Malaysia, were most abundant in polluted drains containing 1.0 to 2.0 g/liter of dissolved oxygen, 1.0-2.4 g/liter of soluble reactive phosphate, and 0.1-0.9 g/liter of ammoniacal nitrogen (Hassan et al. 1993).

In Africa, similar studies with malaria vectors *An. gambiae* Giles s.s and *An. arabiensis* Patton have yielded variable results. While some studies failed to detect any significant relationship between *An. gambiae* s.l. and

environmental variables (Minakawa et al. 1999), others have reported significant relationships. For example, in Eritrea, *An. arabiensis* was associated with shallow, clean water and sunlit habitats (Shililu et al. 2003) as were those reported for *An. gambiae s.s.* in western Kenya (Munga et al. 2005). Fluctuations in physico-chemical factors of the rice field environment during the course of the rice growing cycle also impacted significantly on temporal distribution and abundance of *An. arabiensis* (Muturi et al. 2007a).

Despite the importance of *Cx. quinquefasciatus* in transmission of Bancroftian filariasis in Kenya (Mwandawiro et al. 1997), little is known about its larval ecology. Few studies have reported a significant association between the genus *Culex* and environmental factors such as pH, canopy coverage, debris coverage (Minakawa et al. 1999), and decaying organic matter (Asimeng and Mutinga 1993), with little attempt to assess the effect of these factors on species population dynamics (Muturi et al. 2007a).

A preliminary study aimed at understanding the biology of anophelines prior to implementation of a malaria vector control program in Mwea Irrigation Scheme, Kenya, revealed *Cx. quinquefasciatus* to be a predominant nuisance species and a potential vector of filariasis and arboviruses in the area (Muturi et al. 2006). Further studies revealed that this species thrives in a variety of aquatic habitats including rice fields, canals, seepage areas, ditches, marshes, pits, and temporary pools (Muturi et al. 2007a,b). The objective of this study was to characterize the physico-chemical and biotic factors of these mosquito larval habitats and to identify the factors that influence the abundance and distribution of *An. arabiensis* and *Cx. quinquefasciatus* in diverse aquatic habitats.

MATERIALS AND METHODS

Study area

The Mwea Rice Irrigation Scheme is located 100 km northeast of Nairobi in a riverine plain southeast of Mount Kenya at an altitude of about 1,200 m. A full description of the area is given by Muturi et al. (2006). The study area has two annual rainfall seasons, the long rains in April/May and the short rains in October/November. The average annual rainfall, temperature, and relative humidity is 950 mm (range: 356-1,626 mm), 21.3°C (range: 16.0-26.5° C), and 59.5% (range: 52-67%), respectively. The 1999 Kenya National census estimated the number of individuals in this area to be 150,000 and the number of households to be 25,000. The Rice Scheme covers an area of about 13,640 ha, more than 50% of which is used for irrigated rice cultivation and the remaining area is used for subsistence farming, grazing, and community activities.

Kangichiri village, located within the scheme was selected for this study. The village has approximately 150 homesteads with approximately 650 residents. More than 90% of the houses have mud walls with iron roofing. Cows, goats, chickens, and donkeys are the primary domestic animals kept in the village. Their sheds are generally located within 5 m of most houses. More than 75% of the village land

is under rice cultivation and human habitation occupies the remaining area with less than 10% utilized for growing a variety of vegetables and bananas. The typical rice cultivation cycle includes a land preparation-transplanting period (July-August), a growing period (August-November), and a post-harvest period (November-December).

Sampling of mosquito larvae and non-mosquito invertebrates

Mosquito larval samples were collected over a six-week period between May and June, 2006. The collections were done in all non-paddy aquatic habitats and ten randomly selected paddies and associated canals located within a 200 m radius of the village. The habitats were sampled for mosquito larvae twice per week and up to 20 dipper samples, depending on the size of the aquatic habitat, were taken using a standard mosquito dipper (350 ml). Mosquito larvae were sorted by genus and the 3rd and 4th instars were preserved in 100% ethanol. The larvae were later identified microscopically to species using the taxonomic keys of Hopkins (1952) and Gillies and Coetzee (1987).

The non-mosquito aquatic invertebrates collected in the dipper samples, along with mosquito larvae at each habitat, were also preserved in 100% ethanol and later identified to family using taxonomic keys of Merritt and Cummins (1996). The number of individuals of each family identified were counted and recorded.

Larval habitat characterization

Aquatic habitats were classified based on their size and appearance. A small excavation filled with water was defined as a pool and a low-lying wet land with grassy vegetation was defined as a marsh. An irrigated or flooded field where rice is grown was classified as a paddy and the long and narrow strip of water made for paddy irrigation was defined as a canal. The environmental variables recorded from each sampling site when each sample was collected included; water depth, turbidity, salinity, total dissolved solids (TDS), pH, temperature, conductivity, dissolved oxygen, distance to the nearest house, floating, emergent and submerged vegetation cover, and habitat type. Distance of the sampling site to the nearest house was measured with a tape when it was shorter than 50 m. When the distance exceeded 50 m, it was estimated visually. Emergent vegetation cover was defined as the proportion of the water surface area that was covered by emergent vegetation. Floating vegetation cover was estimated as the proportion of the water surface area that was covered by floating vegetation. Any plant below the water surface was classified as submerged vegetation, and the proportion of water surface area covered by this vegetation was estimated. Water turbidity was estimated visually against a white background and classified as either clear, less turbid, or turbid. The pH, conductivity, dissolved oxygen, and temperature were measured using a hand-held YSI 650 Multi-Parameter Display System (YSI Environmental, YSI Incorporated, Yellow Springs, OH, U.S.A.). Salinity and TDS were measured using field hand-held equipment YSI EC 300 (YSI Environmental, YSI Incorporated, Yellow

Springs, OH, U.S.A.).

Data analyses

Data were analyzed using SPSS version 11.5 (SPSS, Inc., Chicago, IL, U.S.A.) and SYSTAT version 11 (SYSTAT Software Inc, San Jose, CA, U.S.A.) statistical packages. The relative abundance of mosquitoes was expressed as the number of mosquito larvae and pupae per 20 dips because larval and pupal counts were low. The degree of association between *Anopheles* and *Culex* larvae in the aquatic habitats was tested by chi-square. The differences in larval counts among habitat types were compared by repeated measures analysis of variance (ANOVA). Variation in habitat characteristics based on the presence or absence of *An. arabiensis* and *Cx. quinquefasciatus* was compared using ANOVA test for continuous variables and chi-square for categorical variables. Where significant differences were obtained in ANOVA test, the means were separated by Tukey's HSD test. Forward multiple regression analysis was used to obtain the best predictor variables explaining the abundance of the mosquito larvae. Statistical analysis was done after a log transformation $\log_{10}(n+1)$ of larval abundance values to normalize the distribution and minimize the standard error (SE).

RESULTS

Species composition and abundance of mosquitoes and other aquatic invertebrates

In total, 528 collections were made at 44 sampling sites, representing four habitat types; paddies (n=10), canals (n=10), pools (n=16), and marshes (n=8). During the 528 sampling visits, the sampling sites contained water on 348 visits. *Anopheles* larvae were collected in 176 samples, 71 of which had *Anopheles* alone. *Culex* larvae were found in 149 collections and 44 of these collections were exclusively *Culex* sp. Combinations of both *Anopheles* and *Culex* larvae were found in 105 collections. Chi-square analysis indicated that *Anopheles* and *Culex* larvae were more likely to co-exist in the same sampling site than would be expected by chance alone ($\chi^2 = 46.21$, $P < 0.01$). The mean number of *Anopheles* larvae collected was 4.23 (SE = ± 1.01) per 20 dips and the mean number of *Culex* larvae was 12.63 (SE = ± 2.91) per 20 dips. Pupal counts averaged 1.91 (SE = ± 0.75) per 20 dips.

A total of 1,974 larvae was examined microscopically and identified morphologically to species. The collections yielded four mosquito species dominated by *Cx. quinquefasciatus* (73.2%) and *An. arabiensis* (25.0%). The other two species were *Culex annulioris* Theobald (1.3%) and *Culex tigripes* Grandpre and Charmoy (0.5%). *Anopheles arabiensis* and *Cx. quinquefasciatus* were represented in all four habitat types and *Cx. annulioris* and *Cx. tigripes* were found only in pools and canals (Table 1). Repeated measures ANOVA and Tukey's HSD tests revealed that *An. arabiensis* larval abundance did not vary significantly among habitat types ($F = 0.72$, $df = 3, 11$, $P > 0.05$), but *Cx. quinquefasciatus* larval abundance was significantly higher in pools compared with the other habitat types ($F = 6.32$, $df = 3, 11$, $P < 0.05$).

Table 2 shows the distribution of other aquatic invertebrates in different habitat types. Thirteen insect families belonging to five orders were collected (n = 955). These were mainly dominated by Dytiscidae (35.5%), Ephemeroidea (29.4%), Belostomatidae (8.2%), Hydrophilidae (5.9%), and Notonectidae (4.7%). Mites (Acari) and snails (Mollusca) were also encountered occasionally and together with the other insect groups, they accounted for the remaining 16.4% of the total collection. Paddies and canals were the most diverse in terms of the number of insect families and other aquatic arthropods collected, whereas pools were the least diverse.

Larval habitat characteristics

The physico-chemical characteristics of the four habitat types are represented in Table 3. Overall, paddies were located the furthest distance from the nearest homestead and were also characterized by low values of TDS, high amounts of emergent and floating vegetation cover, and cooler turbid waters. Canals were deep habitats with less turbid waters, low values of TDS, less emergent vegetation cover, and high amounts of floating vegetation cover. Marshes were deep, clean water habitats closer to human habitation and contained low amounts of floating vegetation cover, high amounts of emergent vegetation cover, and high TDS values. Pools were the shallowest, warmest and most turbid habitats with small amounts of floating and emergent vegetation cover and high TDS values.

The characteristics of *An. arabiensis* and *Cx. quinquefasciatus* larval habitats are summarized in Table 4. *Culex quinquefasciatus* larval habitats differed from *An. arabiensis* larval habitats in water conductivity and the average number of other aquatic invertebrates collected in the habitats. *Culex quinquefasciatus* habitats had higher water conductivity values and higher abundance of other aquatic invertebrates compared with *An. arabiensis* habitats ($F = 4.562$ and 9.950 , $df = 3, 114$, $P < 0.05$). Habitats with both species differed from habitats with either species in the presence of emergent vegetation (less common in habitats with both species) and distance to the nearest house (habitats with both species were closer to human habitation, $F = 5.497$ and 8.553 , $df = 3, 209$, $P < 0.05$).

Relationship between mosquito larval abundance and environmental variables

Forward multiple regression analysis was used to analyze the effect of various parameters on the relative abundance of immature stages of *An. arabiensis* and *Cx. quinquefasciatus*. The model included 26 variables; 13 physico-chemical variables and 13 insect families that were identified in the samples. Significant models explaining 30.1% and 48.9% of the relative abundance of *Cx. quinquefasciatus* and *An. arabiensis*, respectively, were fitted by the regression model. Seven of the 26 parameters were significantly associated with the relative abundance of immatures of at least one of the two mosquito species. These included dissolved oxygen, emergent vegetation, and TDS among the physico-chemical parameters and Haliplidae, Heptageniidae, Chironomidae,

Table 1. Species composition and abundance (counts/20 dips) of mosquito species collected in different habitat types in Kangichiri village, Mwea, Kenya.

Habitat type	No. of sites	<i>Cx. quinquefasciatus</i>	<i>An. arabiensis</i>	<i>Cx. annulioris</i>	<i>Cx. tigripes</i>
Paddy	10	2.33 ± 1.15	3.11 ± 1.71	NF	0.09 ± 0.04
Canal	10	8.43 ± 4.71	2.27 ± 1.04	0.62 ± 0.62	NF
Pool	16	36.35 ± 12.62	7.04 ± 2.27	0.08 ± 0.05	0.08 ± 0.05
Marsh	8	0.88 ± 0.88	0.31 ± 0.31	NF	NF
Total	44	9.39 ± 2.64	3.28 ± 0.96	0.16 ± 0.15	0.06 ± 0.02

NF: Indicates that the species was not found in respective habitat type.

Table 2. Relative abundance (counts/20 dips) of non-mosquito aquatic invertebrates in different habitat types in Kangichiri village, Mwea, Kenya.

Insect family	Habitat type				
	Paddy	Canal	Pool	Marsh	Total
Hydrophilidae	0.31	0.14	0.85	0.38	0.36
Haliplidae	0.08	0.00	0.12	0.00	0.06
Dytiscidae	2.47	2.49	1.65	1.25	2.19
Curculionidae	0.09	0.11	0.00	0.56	0.13
Libellulidae	0.12	0.35	0.00	0.00	0.14
Coenagrionidae	0.03	0.19	0.04	0.13	0.08
Ephemeridae	2.20	1.59	0.65	2.50	1.82
Heptageniidae	0.16	0.19	0.00	0.06	0.13
Chironomidae	0.07	0.19	0.58	0.13	0.19
Notonectidae	0.29	0.16	0.15	0.81	0.29
Corixidae	0.24	0.32	0.00	0.06	0.20
Belostomatidae	0.52	0.54	0.20	0.19	0.51
Microvelidae	0.04	0.08	0.00	0.00	0.04
Snails	0.01	0.05	0.00	0.13	0.03
Mites	0.03	0.00	0.00	0.00	0.01

and Microveliidae among the potential competitors. The relative abundance of *An. arabiensis* larvae was negatively associated with emergent vegetation and Heptageniidae larvae and positively associated with dissolved oxygen and Haliplidae adults. *Cx. quinquefasciatus* larval abundance was negatively associated with emergent vegetation and positively associated with TDS, dissolved oxygen, larvae of Chironomidae, and adults of Microvelidae (Table 5). The other environmental variables were excluded in the model because they had weaker associations with mosquito larval abundance.

DISCUSSION

Results of this study demonstrated co-existence of *An. arabiensis* and *Cx. quinquefasciatus* larvae in the same aquatic habitats at rates greater than would be expected by chance alone. This is in agreement with results from previous

work (Minakawa et al. 1999, Fillinger et al. 2004). Although both species were associated with emergent vegetation cover and dissolved oxygen, they differed in their association with the other five of the seven significant variables. *Anopheles arabiensis* larvae were positively associated with adults of family Haliplidae and negatively associated with larvae of family Heptageniidae, and *Cx. quinquefasciatus* was positively associated with TDS, Chironomidae larvae, and Microveliidae adults. These findings suggest that both biotic and abiotic factors play a significant role in niche partitioning among *Cx. quinquefasciatus* and *An. arabiensis*, which should be considered when designing an integrated vector control program.

Mosquitoes use chemical and biological cues to detect the presence of larval competitors and avoid ovipositing in such habitats (Blaustein and Kotler 1993). Members of the family Heptageniidae feed on detritus (Lamp and Britt 1981) which also constitute the food for mosquito

Table 3. Average values (\pm SE) of the environmental variables used to characterize the aquatic habitats in Kangichiri village, Mwea, Kenya.

Variables	Habitat type			
	Paddy	Canal	Pool	Marsh
Distance (m)	49.20 \pm 2.02	33.92 \pm 2.95	30.54 \pm 2.40	9.38 \pm 0.43
Emergent vegetation cover (%)	38.76 \pm 3.95	30.30 \pm 2.64	25.23 \pm 3.56	51.88 \pm 8.32
Floating vegetation cover (%)	20.35 \pm 3.61	8.11 \pm 2.57	1.15 \pm 0.85	0.00 \pm 0.00
Submerged vegetation cover (%)	0.37 \pm 0.20	0.03 \pm 0.03	0.04 \pm 0.04	0.38 \pm 0.38
Depth (cm)	7.04 \pm 0.28	10.24 \pm 1.07	6.19 \pm 0.56	9.94 \pm 1.26
Salinity (ppt)	17.08 \pm 1.87	23.79 \pm 2.57	21.75 \pm 4.06	26.38 \pm 7.31
Dissolved oxygen (Mg/L)	5.62 \pm 1.52	2.78 \pm 0.62	3.52 \pm 0.95	1.86 \pm 0.77
pH	7.16 \pm 0.06	7.09 \pm 0.05	6.86 \pm 0.07	7.10 \pm 0.09
Conductivity (μ s)	152.17 \pm 10.41	134.91 \pm 14.23	202.57 \pm 26.57	172.84 \pm 30.39
Temperature ($^{\circ}$ C)	27.08 \pm 0.71	27.52 \pm 1.2	29.44 \pm 0.67	24.07 \pm 0.58
Total dissolved solid (ppt)	0.10 \pm 0.01	0.08 \pm 0.01	0.18 \pm 0.02	0.23 \pm 0.04
Invertebrate total	6.63 \pm 0.70	6.41 \pm 0.93	4.69 \pm 0.87	6.19 \pm 0.99
Turbidity	1.99 \pm 0.08	1.78 \pm 0.13	2.38 \pm 0.15	1.25 \pm 0.11

Table 4. Average values (\pm SE) of the measured environmental factors in aquatic habitats with either *An. arabiensis* or *Cx. quinquefasciatus* alone, both species, or none of the mosquito species in Kangichiri village, Mwea, Kenya.

	<i>Cx. quinquefasciatus</i> only	<i>An. arabiensis</i> only	Both	Neither
No. of collections	44	71	105	128
Distance (m)	41.92 \pm 4.56	46.11 \pm 4.60	32.87 \pm 3.67	37.62 \pm 2.12
Emergent vegetation (%)	41.17 \pm 6.14	43.72 \pm 7.39	22.09 \pm 4.71	36.88 \pm 2.92
Floating vegetation (%)	10.00 \pm 7.69	10.61 \pm 6.83	9.61 \pm 4.51	13.11 \pm 2.44
Submerged vegetation (%)	0.17 \pm 0.17	0.67 \pm 0.55	0.30 \pm 0.26	0.15 \pm 0.11
Depth (cm)	9.25 \pm 1.66	8.28 \pm 1.18	8.70 \pm 1.24	7.59 \pm 0.36
Salinity (ppt)	22.35 \pm 3.22	21.64 \pm 4.03	17.33 \pm 3.00	20.72 \pm 2.05
Dissolved oxygen (Mg/L)	7.23 \pm 5.22	8.23 \pm 3.41	9.20 \pm 3.02	1.97 \pm 0.33
pH	6.80 \pm 0.11	6.90 \pm 0.17	6.85 \pm 0.08	7.20 \pm 0.03
Conductivity (μ s)	192.54 \pm 39.00	106.82 \pm 20.13	153.98 \pm 23.63	164.97 \pm 9.72
Temperature ($^{\circ}$ C)	26.64 \pm 0.95	27.88 \pm 1.94	29.88 \pm 1.95	26.65 \pm 0.46
TDS (ppt)	0.14 \pm 0.03	0.11 \pm 0.02	0.10 \pm 0.02	0.13 \pm 0.01
Other invertebrates	10.67 \pm 1.90	4.61 \pm 0.94	5.35 \pm 0.74	6.15 \pm 0.57
Habitats with clear water (%)	25.0	27.8	39.1	32.1

Table 5. Multiple regression analysis of the abundance of *An. arabiensis* and *Cx. quinquefasciatus* in relation to measured biotic and abiotic characteristics.

Species	Environmental variables	Coefficients	P values
<i>An. arabiensis</i>	Dissolved oxygen (mg/l)	0.679	0.000
	Haliplidae	0.212	0.001
	Heptageniidae	-0.244	0.001
	Emergent vegetation	-0.147	0.013
<i>Cx. quinquefasciatus</i>	Chironomidae	0.382	0.000
	Microveliidae	0.263	0.000
	Dissolved oxygen (mg/l)	0.183	0.009
	Emergent vegetation	-0.173	0.015
	Total dissolved solids (ppt)	0.144	0.041

larvae. Our findings seem to indicate that gravid females of *An. arabiensis* would avoid ovipositing in habitats where members of family Heptageniidae are present, presumably to avoid direct competition. Kramer and Garcia (1989) observed a positive relationship between mosquito larvae and other predators. However, none of the insect families that were significantly associated with mosquito larvae in the current study is known to compete with or prey on mosquito larvae. Because most insect predators are generalized in their diet (Mogi 1978) they may prey on individuals across these families. Our findings suggest that habitats in which mosquito larvae are abundant are also attractive to other aquatic invertebrates that are preyed upon by similar predators. Interestingly, the most abundant insect families were not significant predictors of mosquito larval abundance, an indication that other factors besides numbers are important in determining the outcome of interspecific interactions. Although our sampling may have been biased in collection of some aquatic invertebrates, these findings underscore the need to understand how mosquito larvae interact with other aquatic insects when formulating a vector control program with the aim of preserving the natural sources of mosquito larval mortality.

Emergent vegetation is known to have direct effects on some mosquito species by obstructing gravid females from ovipositing and supporting a greater diversity of aquatic predators (Rajendran and Reuben 1991, Grillet 2000). Emergent vegetation may also reduce the amount of sunlight reaching the water surface, resulting in lower temperatures. Reduced temperatures cause a decline in microbial growth upon which mosquito larvae depend on and increases the larval development time exposing them to greater risks of contact with potential predators and competitors (Ramachandra-Rao 1984). To avoid these difficulties, *An. arabiensis* is known to prefer open sunlit habitats without vegetation for oviposition (Gimnig et al. 2001, Shililu et al. 2003) and the pattern appears to be the

same for *Cx. quinquefasciatus*.

Several studies have examined the influence of dissolved oxygen concentration on the abundance of *Anopheles spp.* and *Culex spp.* with contradicting results. Grillet (2000) reported a positive association between dissolved oxygen and the abundance of *An. oswaldoi* and Amerasinghe et al. (1995) reported a negative association between dissolved oxygen and *An. culicifacies*. Similarly, Senior-White (1926) reported *Cx. vishnui* from hyper-oxygenated water, a finding that has recently been confirmed by Sunish and colleagues (2006). However, it remains unknown whether it is oxygen per se or an associated physico-chemical or abiotic factor that influences the abundance of mosquito species. Sunish et al. (2006) suggested that high algal productivity and associated photosynthesis is responsible for high dissolved oxygen concentrations in aquatic habitats, thereby favoring higher survival of mosquito larvae. In the current study, we did not quantify the amount of algal growth, but considering that the majority of the sampled habitats had *Azolla sp.* and other floating and submerged vegetation which consists mainly of algal biomass, it is likely that algal productivity resulted in higher concentration of dissolved oxygen, thereby promoting larval productivity. TDS, which is the sum of all dissolved organic, inorganic, and suspended solids in water, was also a significant factor in productivity of *Cx. quinquefasciatus*. In most areas of its distribution, *Cx. quinquefasciatus* prefer habitats rich in dissolved matter (Hassan et al. 1993) and such habitats tend to have high TDS.

Habitats in which both *An. arabiensis* and *Cx. quinquefasciatus* co-existed differed from those that harbored either of the two species. Habitats with both species were closer to human habitation and were less likely to have emergent vegetation than those with either of the two species. The results also indicated that *Cx. quinquefasciatus* was able to thrive in habitats with higher density of other aquatic invertebrates compared with *An.*

arabiensis, suggesting that this species was more tolerant to interspecific associations among aquatic invertebrates than *An. arabiensis*. Considering that emergent vegetation was a significant predictor of both *An. arabiensis* and *Cx. quinquefasciatus*, the results suggest that the two species are likely to exploit the habitat characteristics that are strongly associated with either species. Gimnig et al. (2001) observed a similar trend between *An. arabiensis* and *An. gambiae* s.s. This phenomenon is likely to benefit both species particularly in the more complex habitats such as paddies and canals where the diversity of other aquatic invertebrates, including potential predators, was great.

Although the complex community structure of the rice fields and canals does not support higher mosquito density as do the less complex habitats such as pools, they are capable of holding water for a longer period than the pools, making them important larval habitats over time. Previous studies have shown that a large number of low density, but continuously productive, habitats contribute more to the density of adult mosquito populations than single high density larval habitats (Grillet 2000). This underscores the need to exhaustively target all the larval habitats regardless of their larval densities.

The specific cues that trigger oviposition behavior in mosquitoes are largely unknown. It has been suggested that a large number of variables may be correlated with other characteristics that act as cues for ovipositing females (Gimnig et al. 2001). Because of methodological and logistical difficulties, the current study had several limitations. First, it is possible that the estimated environmental variables were correlated with other factors that were not considered in this study. Secondly, the study was conducted over a six-week period after which time all the aquatic habitats dried up. Although this design provided essential information on environmental factors that regulate mosquito population in temporary aquatic habitats, this period was too short to establish the temporal changes in larval habitats. Thirdly, it was also problematic to compare the productivity of larger habitats such as paddies, canals, and marshes with the smaller pools due to variation in the number of dips collected. To standardize the results, we estimated the larval abundance as larval counts per 20 dips. Although this method is widely used in larval sampling, it may have overestimated the larval counts in small pools. Finally, the diversity of other aquatic invertebrates was estimated from the dipper samples and this may have underestimated both the species diversity and abundance. A more comprehensive study targeting a large number of variables and a more elaborate method of estimating the diversity of other aquatic invertebrates over a longer period of time is warranted.

In summary, this study has established the habitat characteristics of *Cx. quinquefasciatus* and *An. arabiensis* in a rice agro-ecosystem in Mwea Kenya. The study has established that although both species may exploit the same habitats for larval development, they respond differently to habitat factors resulting in niche partitioning. These results provide useful information that can be used as a guide for designation and implementation of an integrated vector

control program.

Acknowledgments

We are grateful to Prof. Christian Borgemeister, Director General, International Centre of Insect Physiology and Ecology, for his strong support in this project. We acknowledge the data collection provided by Simon Muriu, Peter Barasa, Enock Mpanga, James Wauna, Peter M. Mutiga, William Waweru, Nelson Maingi, Martin Njigoya, Paul K. Mwangi, Christine W. Maina, Isabel M. Marui, Gladys Karimi, Irene Kamau, Susan W. Mugo, Nicholas Gachoki, Charles Kiura, and Naftaly Gichuki. This research was supported by NIH/NIAID grant # U01A1054889 (Robert Novak).

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