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Contribution of different aquatic habitats to adult *Anopheles arabiensis* and *Culex quinquefasciatus* (Diptera: Culicidae) production in a rice agroecosystem in Mwea, Kenya

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ABSTRACT: Studies were conducted to determine the contribution of diverse larval habitats to adult *Anopheles arabiensis* Patton and *Culex quinquefasciatus* Say production in a rice land agro-ecosystem in Mwea, Kenya. Two sizes of cages were placed in different habitat types to investigate the influence of non-mosquito invertebrates on larval mortalities and the contribution of each habitat type to mosquito productivities, respectively. These emergence traps had fine netting material covers to prevent adult mosquitoes from ovipositing in the area covered by the trap and immature mosquitoes from entering the cages. The emergence of *Anopheles arabiensis* in seeps, tire tracks, temporary pools, and paddies was 10.53%, 17.31%, 12.50%, and 2.14%, respectively, while the corresponding values for *Cx. quinquefasciatus* were 16.85% in tire tracks, 8.39% in temporary pools, and 5.65% in the paddies from 0.125 m^3 cages during the study. Cages measuring 1 m^3 were placed in different habitat types which included paddy, swamp, marsh, ditch, pool, and seep to determine larval habitat productivity. *An. arabiensis* was the predominant anopheline species (98.0%, n=232), although a few *Anopheles coustani* Laveran (2.0%, n=5) emerged from the habitats. The productivity for *An. arabiensis* larvae was 6.0 mosquitoes per m^2 for the temporary pools, 5.5 for paddy, 5.4 for marsh, 2.7 for ditch, and 0.6 for seep. The *Cx. quinquefasciatus* larval habitat productivity was 47.8 mosquitoes per m^2 for paddies, 35.7 for ditches, 11.1 for marshes, 4.2 for seeps, 2.4 for swamps, and 1.0 for temporary pools. Pools, paddy, and marsh habitat types were the most productive larval habitats for *An. arabiensis* while paddy, ditch, and marsh were the most productive larval habitats for *Cx. quinquefasciatus*. The most common non-mosquito invertebrate composition in the cages included Dytiscidae, Notonectidae, Belostomatidae, and Ephemerellidae, and their presence negatively affected the number of emergent mosquitoes from the cages. In conclusion, freshly formed habitats are the most productive aquatic habitats, while old and more permanent habitats are the least productive due to natural regulation of mosquito immatures. ***Journal of Vector Ecology* 33 (1): 129-138. 2008.**

Keyword Index: Predation, *An. arabiensis*, *Cx. quinquefasciatus,* emergence rate, productivity, mosquitoes.

INTRODUCTION

Mosquito populations are regulated by a variety of factors, including adverse climatic conditions, limited food supply, competition, parasites, pathogens, and predators (Service 1973). The importance of any one of these factors in different environments is poorly understood, thus affecting proper understanding of the factors that affect production of adult populations. Predation is recognized as an important factor in the organization of many ecological communities (Sih et al. 1985), including aquatic communities (Zaret 1980). Together with insect pathogens, predation can significantly limit numbers of mosquitoes depending on the species and type of habitat.

Mosquito larvae and their predators co-exist in a variety of aquatic habitats ranging from large and permanent sites to small and temporary collections of water. Service (1977) observed higher mortality of immature stages of *An. gambiae* Giles in the rice fields than in small pools and ponds. This was attributed to higher density and diversity of predators in rice fields than in rain pools and ponds. He further analyzed the gut contents of possible predators by precipitin tests and showed that members of the orders Coleoptera, Hemiptera, and Diptera were important mosquito larval predators. Jenkins (1964) found that some Hemipterans tested, such as species of *Laccotrephes, Enithares,* and *Anisops* and various Corixids, produced a positive reaction to *An. gambiae* antisera suggesting that they were important predators. In Tanzania, Christie (1958) observed high predation pressure by Notonectidae on mosquito larvae and pupae. In Japan, Notonectidae and *Chaoborus* species (Diptera) were found to be predators of mosquito larvae (Toshihiko et al. 2002).

The rate at which new individuals are produced is one of the key factors that determine the growth rate of insect populations. This rate is critically dependent on the growth characteristics of immature stages, which is governed by temperature when food is not limiting (Lassiter et al. 1995). In general, within the limits of a lower development threshold and an upper lethal temperature, the aquatic stages of mosquitoes develop faster as temperature increases (Brust 1967, Hagstrum and Workman 1971, Lyimo and Takken 1993). The shortening of aquatic life is important since it will increase adult turnover, with consequences for increased vector biting rates and disease transmission (Garret-Jones 1964). Importantly, production of adult mosquitoes is not directly proportional to the rate of development of the aquatic stages, since at temperatures that result in the fastest rate of development, fewer adults are produced (Bayoh and Lindsay 2003, 2004). In natural habitats, higher temperatures shorten larval development time, but accelerate the drying of habitats so as to reduce their contribution to adult mosquito production, while lower temperatures increase the duration of life cycle and increase the probability of encountering natural enemies (Speight et al. 1999). 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 also increases the number of places larvae can hide from predators, consequently increasing the probability of larval survivorship.

Ovipositing female mosquitoes are known to choose among water bodies based on cues such as temperature, light, water depth, turbidity, and presence of competitors (Bentley and Day 1989, Lee 1991). Mosquitoes avoid ovipositing where interspecific competitors are present (Blaustein and Kotler 1993) but are attracted to sites where other mosquito larvae are present (Beehler and Mulla 1995). The presence of conspecific larvae may provide a reliable cue that a pond offers suitable conditions for larval development (Stav et al. 1999, Mokany and Shine 2003). Mosquitoes use chemical and physical cues to detect ponds where conspecific larvae are present (Millar et al. 1994, Takken 1999) including traits such as salinity, dissolved oxygen, and organic matter (Lee 1991). Chemical and biological cues are also used by mosquitoes to detect the presence of larval predators and competitors in ponds (Petranka and Fakhourry 1991, Beehler et al. 1994, Spencer et al. 2002). Mosquitoes may avoid ovipositing in water bodies where a fungus commonly associated with a competitor is present.

Estimating larval habitat productivity has been based on two methods: pupal counting and emergence traps (Munga et al. 2006, Mutuku et al. 2006). Each method has its merits and shortcomings. Pupal counting yields a direct measurement of pupal production of a habitat, but logistically it is difficult in large habitats and substantial errors may occur when the habitats contain aquatic vegetation in which the pupae may be concealed. This method also has a methodological issue on standardization between different investigators counting pupae in the habitat, where the number of pupae depends on how thorough the investigator examines the habitat. On the other hand, emergence traps are easy to deploy and the number of adults recovered can be readily standardized (Service 1993). The habitat types within the Mwea Irrigation scheme include rice paddies, canals, seeps, marshes, ditches, and hoof prints (Mukiama and Mwangi 1990, Mutero et al. 2000, Mutero et al. 2004b, Muturi et al. 2006, Mwangangi et al. 2006a, Jacob et al. 2007a). Most entomological studies in this area have concentrated on larval abundance within the habitats and the seasonal and spatial distribution of adult mosquitoes in the houses. None of these studies has addressed the issue of mosquito production from the habitats. The objective of this study was to determine the contribution of different aquatic habitats to adult *Anopheles arabiensis* and *Culex quinquefasciatus* productivity in a rice agro-ecosystem in Mwea, Kenya. We hypothesized that different aquatic habitats contribute disproportionately to adult mosquito numbers in the Mwea Irrigation Scheme.

MATERIALS AND METHODS

Study area

The study was conducted between April and December, 2005, in the Mwea Irrigation Scheme (MIS), in Kirinyaga District, approximately 100 km northeast of Nairobi, Kenya. This area has been previously described (Mukiama and Mwangi 1989, Mutero et al. 2000, Mutero et al. 2004b, Jacob et al. 2006, Muturi et al. 2006, Mwangangi et al. 2006a, Jacob et al. 2007b, Muturi et al. 2007b). Mwea occupies the lower altitude zone of Kirinyaga District in an expansive low-lying area mainly characterized by black cotton soil. The mean annual rainfall is 950 mm with long rains in April/May and short rains in October/November. The average temperatures are in the range of 16 – 26.5° C and relative humidity varies from 52-67%. According to the 1999 national census, Mwea division has an estimated 150,000 persons in 25,000 households. The Mwea Irrigation Scheme is located in the west-central region of the Mwea division and covers an area of about 13,640 ha. Over 50% of the scheme area is used for irrigated rice cultivation while the remaining area is used for subsistence farming, grazing, and community activities.

Two separate experiments were conducted, one in the Mwea Irrigation and Agricultural Development Centre (MIAD) located in the MIS and one in Kiamachiri village which is located approximately 2 km outside the scheme and within the "unplanned" rice growing area. MIAD Centre is a rice research field station in which farming follows a definite rice-cropping cycle stipulated by MIS. 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). The second crop is cultivated prior to the long rain period between January and May.

In the village of Kiamachiri, rice farming covers approximately 20% of the total area. Rice is grown throughout the year along the River Gakungu that flows on the edge of the village (unplanned rice cultivation). On average, most paddies in this village measure 20 m by 40 m, although the sizes vary depending on water amounts available and distance from the river valley. The village has approximately 850 inhabitants living in about 200 homesteads. The common domestic animals found in this area are cattle, donkey, goats, sheep, and chicken, and they are kept around 5 m from the houses. More than 90% of the houses in this village are mud-walled with metal roofing.

Effect of non-mosquito invertebrates on habitat productivity

Cages measuring 0.125m^3 (50 cm x 50 cm x 50 cm) were placed in different habitats to determine the effect of non-mosquito invertebrates on larval habitat productivity. The cages were placed at different times depending on the rainfall (pools, tire tracks, and seep) and rice growth cycle for paddy habitat type. The sides of each cage were covered with metal sheets to a 30 cm mark to prevent movement of enclosed mosquito immatures in and out of the cage. Further, at every habitat, the cages were pressed in the substrate such that they could support themselves. The cages were placed in temporary pools, tire tracks, seepage, and the paddy habitats and covered with netting material to prevent entry of gravid mosquitoes and other insects. The placement of the cages within the habitat was purposive (i.e., based on visual presence of larvae) and was not random relative to other locations in the habitat. For the paddy habitat, the cages were placed at the edges (Ikemoto 1978, Pitcairn et al. 1994, Mwangangi et al. 2008) and the number of replicates in each paddy was dependent on the water volume. A total of 36 replicates (cages) were placed in seep (8), tire tracks (4), pools (14), and paddy (10). The placement of the cages was based on the availability of the habitat in this area.

Cages were placed two days and three weeks after the onset of the long rains in the non-paddy habitats, and eight weeks post-transplanting in the paddies. Two days after the beginning of the main rain season, the habitats were colonized by mosquitoes. Three weeks after the beginning of rains, the habitats were stable. Eight weeks post-transplanting, the rice was at the late vegetative stage, which is associated with an increase in mosquito larvae and other aquatic invertebrates (Mwangangi et al. 2006a, Muturi et al. 2007b). Effort was made to ensure all the visible mosquito larvae were counted and recorded at day 0. The larvae were collected into a white tray using pipettes and they were counted from the tray. The numbers of larvae in the cages were counted each day until they either emerged into adults or died. Emergent mosquitoes were collected from the cages by aspiration (WHO 1975), placed in paper cups with moist cotton wool, and transported to the laboratory for morphological identification (Edwards 1941, Gillies and Coetzee 1987).

The non-mosquito aquatic invertebrates usually colonize the habitats slower than the mosquitoes. The non-mosquito aquatic invertebrates were qualitatively estimated in the cages by accessing relative abundance of the representative families. Representative samples of non-mosquito invertebrates at each habitat were also preserved in 100% ethanol and later identified to family using taxonomic keys (Merritt and Cummins 1996). The non-mosquito invertebrates were scored in terms of their relative abundance as absent, less abundant, or abundant. An individual family of non-mosquito invertebrates was classified as less abundant if fewer than ten individuals were observed in the cage. If more than ten individuals were present, the family was classified as abundant.

Productivity from different habitats

The productivity of different habitats for mosquitoes was conducted in Kiamachiri village. The cages were designed the same way as in the previous experiment except that they were twice as large (1m x 1m x 1m). This particular cage type was useful in determining the productivity of the aquatic habitat per m^2 per week. The design of the cages (emergence trap) helped to prevent adult mosquitoes from ovipositing in the area covered by the trap and immature mosquitoes from entering the cage. The placement of the cages was based on the visual presence of mosquito larvae. After the cage placement, the enclosed mosquito larvae were counted as described earlier. The cages in which mosquito larvae were enclosed were monitored daily for emergent mosquitoes, which if present, were collected and processed as described before.

A sub-sample of emergent An. gambiae s.l. from both experiments was identified into sibling species using the rDNA PCR technique (Scott et al. 1993). The results of this molecular identification showed that all the identified specimens were An. arabiensis. The non-mosquito invertebrates enclosed within the cages were identified to family level (Merritt and Cummins 1996) and qualitatively assessed and scored for their relative abundance as absent, less abundant, or abundant as described earlier.

Statistical analysis

Statistical analyses were done using SPSS software (Version 15.0 for windows, SPSS Inc., Chicago, IL). The sum of each larval instar was computed from each trial and the emergent mosquitoes were counted. Survivorship from L1 to adult emergence was estimated by A/I, where A = total number of adults and I = total number of immature originally counted at day 0 at each cage.

A negative exponential growth model was used to fit the relationship between observed abundance and cumulative developmental time for each developmental stage in the cages in different habitats placed in MIAD.

One-way analysis of variance (ANOVA) was used to compare the differences in the number of emergent mosquitoes in different habitats. Where significant differences were detected in ANOVA, Tukey-Kramer honestly significant difference (HSD) was used to compare the differences between means. A paired sample t-test was used to compare the differences between *An. arabiensis* and *Cx. quinquefasciatus* adult emergence. Statistical analysis was done after arcsine transformation of emergent mosquito rate values to normalize the distribution and minimize the standard error.

RESULTS

Immature and emergence mosquitoes from cages at different periods in MIAD

Table 1 shows the number of mosquito immatures enclosed in the cages during different periods. Two days after the rains, the cages had a total of 1,112 *Anopheles* larvae of which 96 (8.63%) were in cages in seeps, 174 (15.65%) in tire tracks, and 842 (75.72%) in pools. No pupae and *Culex* larvae were found in the habitats at this period. When the cages were placed three weeks after the rains, a total of 1,072 mosquito larvae were observed. These included 567 (52.89%) anophelines and 505 (47.11%) culicines. Both anopheline and culicine larvae were observed in all habitat types except in seeps which had only anopheline larvae (n=19). A total of 207 mosquito larvae were found in the cages in paddy habitats ten weeks post-transplanting.

Table 2 shows the emergence of mosquitoes in different habitats during the study period. *An. arabiensis* had colonized the habitats two days after the long rains and was the only mosquito species present at this time. Two days after the onset of rains, a total of 382 *An. arabiensis* adults emerged from the cages, of which 283 (74.08%) were from the temporary pools, 73 (19.11%) tire tracks, and 26 (6.81%) seeps. With the absence of non-mosquito invertebrates, the overall emergence was significantly higher in the tire tracks (41.95%) compared to seeps (27.08 %) and temporary pools (33.61%) (F = 55.05, df= 1,5, P=0.002). At this time, the culicine mosquitoes had not colonized the newly-formed habitats. Three temporary pools, lasted for about two weeks and the emergence of *An. arabiensis* was quite high (range 84.00 – 97.87). It took ten days for all mosquitoes in the temporary pools to emerge, but the majority of pools lasted for six days resulting in fewer emergent mosquitoes. The emergent mosquitoes comprised 66.75% (n=382) females of *An. gambiae* s.l. and the rest were males. rDNA PCR analysis of 200 specimens of *An. gambiae* s.l. indicated *An. arabiensis* to be the only sibling species present.

Three weeks after the onset of rains, *An. arabiensis* Patton was found to co-exist with culicine mosquitoes and other aquatic invertebrates. Out of 151 mosquitoes that emerged from the cages, 78 (51.66%) were *An. arabiensis* and 73 (48.34%) were *Cx. quinquefasciatus*. The emergence rate for *An. arabiensis* adults was 10.53% in seeps, 17.31% in tire tracks, and 12.50% in temporary pools. The emergence rate for *Cx. quinquefasciatus* Say adults was 16.85% in tire tracks and 8.39% in temporary pools. There was no significance difference in emergent mosquitoes from different habitats for *An. arabiensis* (p = 0.212) and *Cx. quinquefasciatus* (p = 0.194). Of the 78 emergent *An. arabiensis* adults, 64.10% were females and the rest were males. In contrast, *Cx. quinquefasciatus* males accounted for 68.49% of the 73 individuals of this species collected.

The paddy habitats enclosed within the cages eight weeks post-transplanting were colonized with mosquitoes along with other aquatic invertebrates. During this period of rice growth, only nine mosquitoes emerged of which two (22.22%) were *An. arabiensis* and seven (77.78%)

Table 1. The number of mosquito immatures found in cages in different habitat types during different periods in MIAD.

Cage placement	**Habitat type (replicates)**	Immatures				**Total**
		Early Instars ***An. arabiensis***	**Late instars** ***An. arabiensis***	**Early Instars** ***Cx. quinquefasciatus***	**Late Instars** ***Cx. quinquefasciatus***	
2 days after rain	Seeps (4)	62	34	0	0	96
	Tire tracks (2)	114	60	0	0	174
	Pools (7)	546	296	0	0	842
3 weeks after rain	Seeps (4)	11	8	0	0	19
	Tire tracks (2)	91	65	240	122	518
	Pools (7)	324	68	121	22	535
8 weeks post transplanting	Paddies (10)	74	9	103	21	207

Table 2. Different habitat productivity for *An. arabiensis* and *Cx. quinquefasciatus* at different periods in MIAD.

			Emergent mosquitoes						
Cage placement	**Habitat type (replicates)**	**Larvae**	***An. arabiensis* females**	***An. arabiensis* males**	***Cx. quinquefasciatus* females**	***Cx. quinquefasciatus* males**	**% *An. arabiensis* emergence**	**% *Cx. quinquefasciatus* emergence**	**Other Invertebrates**
2 days after rain	Seeps (4)	96	12	14	0	0	27.08	0.00	A[b]
	Tire tracks (2)	174	55	18	0	0	41.95	0.00	A
	Pools (7)	842	188	95	0	0	33.61	0.00	A
3 weeks after rain	Seeps (4)	19	0	2	0	0	10.53	0.00	+[c]
	Tire tracks (2)	518	22	5	18	43	17.31	16.85	+
	Pools (7)	535	28	21	5	7	12.5	8.39	+
8 weeks post-transplanting	Paddies (10)	207	1	1	2	5	2.41	5.65	++[d]

A[b] Other Invertebrates absent; +[c] Other invertebrates less abundant; ++[d] Other invertebrates abundant.

Table 3. The number of *An. arabiensis* and *Cx. quinquefasciatus* larvae at day zero and the emergent mosquitoes from each habitat type in Kiamachiri.

	Immatures at day 0					Emergent mosquitoes			
Habitat type	**Early instars *Anopheles***	**Late instars *Anopheles***	**Early instars culicine**	**Late instars culicine**	**Pupae**	*An. arabiensis*	*Cx. quinquefasciatus*	***Anopheles* per M²**	**Culicine per M²**
Paddy	492	91	827	57	13	143	1,243	5.50	47.81
Swamp	14	0	160	978	0	0	26	0.00	2.36
Marsh	231	32	440	82	27	65	133	5.40	11.08
Ditch	57	16	175	22	19	8	107	2.67	35.67
Pool	35	8	57	8	1	18	3	6.00	1.00
Seep	10	5	21	30	3	3	21	0.60	4.20
Total	**839**	**152**	**1,680**	**1,177**	**63**	**237**	**1,533**	**3.95**	**25.55**

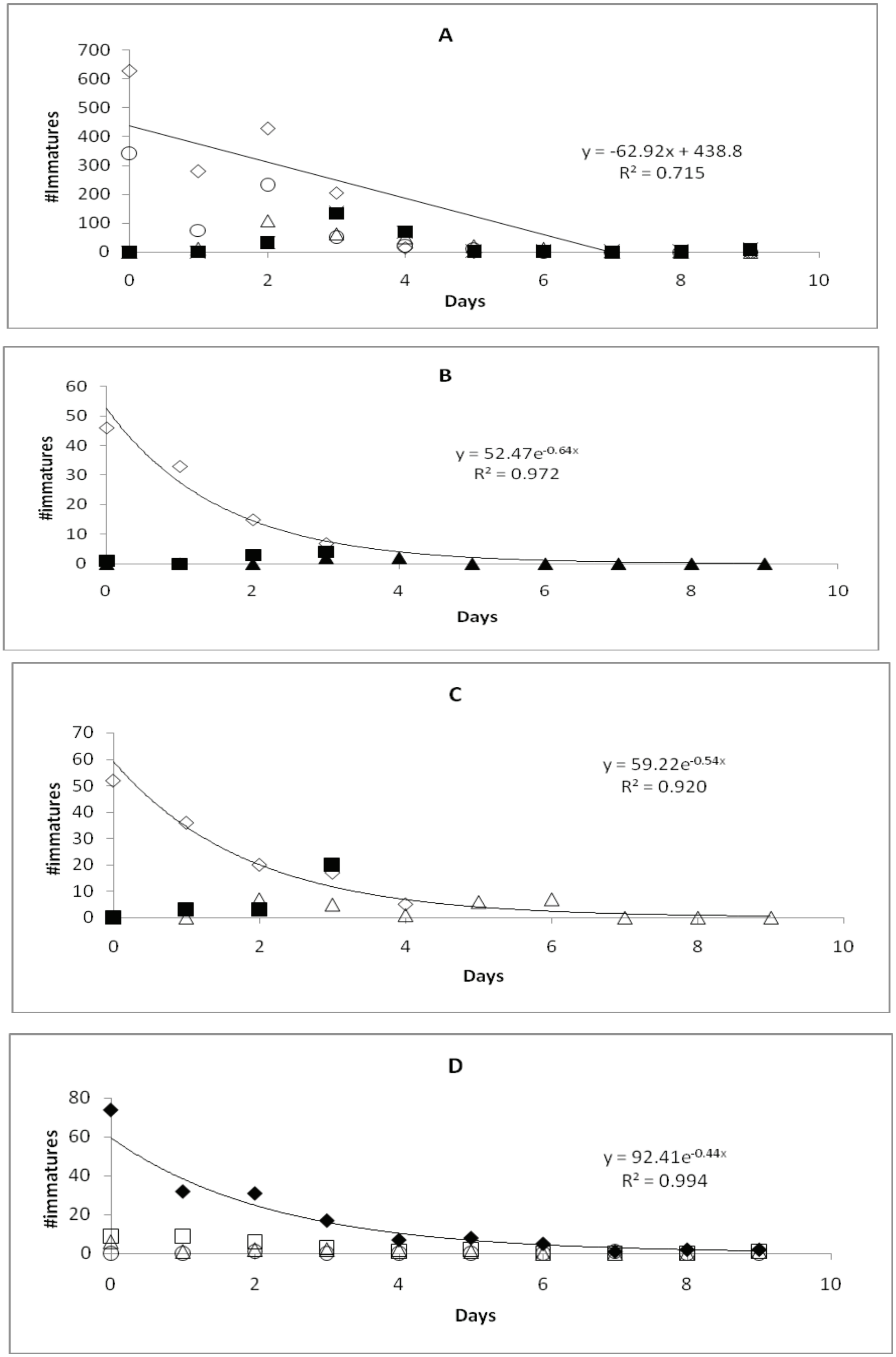

Figure 1. Age distribution and mosquito survivorship curves of *An. arabiensis* in A) Pools, B) Seeps, C) Tire tracks, and D) Paddies in cages in MIAD.

Table 4. The other non-mosquito invertebrates present in cages placed in the paddy habitat type in MIAD.

Order	Family	**Presence**
Hemiptera	Notonectidae	Abundant
	Microvellidae	Less abundant
	Belostomatidae	Abundant
Coleoptera	Dytiscidae	Abundant
	Hydrophilidae	Less abundant
Odonata	Coenagrionidae	Less abundant
	Libullidae	Less abundant
Ephemeroptera	Ephemerellidae	Abundant
Other invertebrates	Snails	Less abundant
	Tadpoles	Less abundant

were *Cx. quinquefasciatus.* The emergence rate of *An. arabiensis* adults was 2.41% (range: 0.00 – 6.67) and that of *Cx. quinquefasciatus* was 5.65% (range: 0.00 – 50.00). At this rice-growing stage, many non-mosquito invertebrates colonized the rice fields. There were fewer of both *Anopheles* and culicine larvae during this period compared to the cages that were placed immediately two days after the beginning of rain. When the cages were placed three weeks after the rains, the habitats were found to contain similar numbers of *Cx. quinquefasciatus* and *An. arabiensis* larvae (t = -1.098, p = 0.289). Vertical survivorship curves were constructed to show the survivorship of immature stages of *An. arabiensis* in different habitat types in MIAD (Figure 1). The estimated mortality rate was highest in pools (0.846), followed by tire tracks (0.959), seeps (0.986), and the paddies (0.997). The mortality rate in the pools was significantly different from the other habitat types (p = 0.005).

Productivity of different habitat types in Kiamachiri village

The habitats, which were enclosed with 1 m^3 cages, included paddies (n=26 cages), swamps (n=11), marshes (n=12), ditches (n=3), pools (n=3), and seeps (n=5). The difference in the number of aquatic habitats of each kind selected for the study was a result of availability. Table 3 shows the number of mosquito larvae present at day 0 and the emerging adult mosquitoes from each habitat type. Among the 137 anophelines collected, *An. arabiensis* accounted for 98.0% and the remaining proportion was comprised of *An. coustani*. All emergent culicine mosquitoes (n=1,533) were identified as *Cx. quinquefasciatus*.

The productivity of larval habitats for *An. arabiensis* per m^2 per week was 6.0 in temporary pools, 5.5 in paddies, 5.4 in marshes, 2.7 in ditches, and 0.6 in seeps. None of the *An. arabiensis* emerged from the swamps. One way ANOVA and Tukey-Kramer HSD tests showed the emergence of *An. arabiensis* in the larval habitats to be significantly higher in temporary pools, paddies, and marshes compared to the other habitats (F = 6.74, df = 1, 5; *P* = 0.027). *Culex quinquefasciatus* habitat productivity per m^2 per week was 47.8 for paddies, 35.7 for ditches, 11.1 for marshes, 4.2 for seeps, 2.4 for swamps, and 1.0 for pools. Paddies and ditches were more productive than the other habitats for *Cx. quinquefasciatus* (F = 16.09, df= 1, 10; *P* = 0.023). Temporary pools were the most productive habitats for *An. arabiensis* and the least productive for *Cx. quinquefasciatus*. Likewise, ditches produced large numbers of *Cx. quinquefasciatus* and very few *An. arabiensis.*

Non-mosquito invertebrates

Among the other non-mosquito invertebrates, Dytiscidae, Notonectidae, Belostomatidae, and Ephemerellidae were the most common in the cages (Table 4). The other non-mosquito invertebrates found within the cages included Coenagrionidae, Libelullidae, and Microvellidae. Snails and tadpoles were also occasionally observed in some of the cages. Whenever these invertebrates occurred in the habitats, low numbers of emergent mosquitoes were witnessed as earlier shown in data in Table 2.

DISCUSSION

An. arabiensis larvae were the first and the only species that were found in the aquatic habitats two days after the rains. The contribution of these pools to adult numbers was dependent on the length of time that they held water, with long-lived pools contributing more than the short-lived ones. Habitat stability is a critical factor influencing mosquito larval survivorship (Minakawa et al. 2005, Mutuku et al. 2006). Habitat stability may be a particularly severe problem for small-sized habitats such as temporary pools. Under high evaporation rates that are characteristic of tropical Africa, the small-sized habitats may dry out before the larvae complete their development. However, warmer water temperatures in these small-sized habitats may also shorten larval development time (Brust 1967, Hagstrum and Workman 1971, Lyimo and Takken 1993). According to studies of Bayoh and Lindsay (2003), adult emergence was highest between 22° C and 26° C. At low temperatures, fewer adults may be produced in the field, due to increased risk of attack by predators and/or disease pathogens (Speight et al. 1999).

The colonization pattern for the freshly-formed habitats was first by *An. arabiensis,* followed by *Cx. quinquefasciatus* and later by non-mosquito invertebrate larvae. Production of adult *An. gambiae s.l.* occurs mainly in small, temporary, sunlit, turbid pools of water (Gimnig et al. 2002). The genus *Culex* has been found to be associated with canopy coverage, debris coverage (Mwangangi et al. 2006a, Muturi et al. 2007a), and decaying vegetable matter (Asimeng and Mutinga 1993), which indicates that the culicine mosquitoes occupy habitats that have had water for longer periods of time.

The mortality rates were 84.56% for temporary pools, 95.92% for tire tracks, 98.59% for seeps, and 99.70% for paddies. Our results are similar to other studies done in the East African Region (Service 1973, Service 1977, Aniedu et al. 1993, Mwangangi et al. 2006b, Munga et al. 2007). The survivorship was better in newly-formed pools compared to paddy habitats that were in existence for a longer period of time. The number of emergent mosquitoes was significantly higher in the absence than in the presence of other invertebrates. Other studies suggest that predation accounts for more than 95% of mortalities in the habitat (Service 1977, Aniedu et al. 1993, Munga et al. 2007). We hypothesize that the non-mosquito invertebrates play a significant role in regulating mosquito immature stages through predation and/or competition at these habitats. Dytiscidae, Notonectidae, Libullidae, and Coenagrionidae were found in the cages and are known to be important mosquito larval predators (Service 1973, Service 1977). The low numbers of both *Anopheles* and *Culex* larvae and the resulting low numbers of emerging adults in long-lived habitats containing many non-mosquito invertebrates is to be expected in nature. When making a choice for oviposition sites, mosquitoes prefer to oviposit in habitats where conspecifics are present and potential predators and competitors are absent (Blaustein and Kotler 1993, Beehler and Mulla 1995). It was also observed that whenever there were high densities of other non-mosquito invertebrates, fewer *An. arabiensis* emerged as adults compared to *Cx. quinquefasciatus*. *Culex* mosquitoes are better able to escape from the attacks of predators compared to *Anopheles*, probably due to the presence of their larval siphon.

Pools, paddies, and marshes were most productive for *An. arabiensis,* and paddies and ditches were the most productive for *Cx. quinquefasciatus*. These cages were placed at the paddy habitat at the early vegetative stage of rice growth. Early vegetative stage of rice growth has been associated with high densities of *An. arabiensis* and *Cx. quinquefasciatus* (Ijumba et al. 1990, Mutero et al. 2000, Mutero et al. 2004a, Mwangangi et al. 2006a). At this stage, water is most exposed due to the low vegetation cover. In this study, the number of emerging *An. arabiensis* and *Cx. quinquefasciatus* decreased when the vegetation cover and floating debris increased. In contrast, habitats with high vegetation cover and debris had more aquatic stages of other invertebrates and this may have increased predation and competition pressure. The structural complexity of habitats and the age of temporal habitats have been shown to influence arthropod populations in both natural and agricultural environments (Rypstra et al. 1999, Yanoviak 2001a, b, Finke and Denno 2002, Carlson et al. 2004). Stable habitats provide favorable conditions for development of other non-mosquito invertebrates that co-exist with mosquito larvae. Due to intra- and interspecific competition for resources, the number of emergent mosquitoes decline significantly. A reduction in the structural complexity of a habitat leads to increase in intraguild predation (Predator-predator antagonism) thus reducing the predation pressure on the prey species. There is a need to further investigate which of the non-mosquito invertebrates observed act as predators of *An. arabiensis* and and *Cx. quinquefasciatus*. In conclusion, during the time period of the studies more mosquitoes emerged from newly-formed habitat types compared to "older" habitat types. For effective larval control programs in the Mwea irrigation scheme, larvicides should target the newly-formed, rain-dependent habitats and paddy habitats at early stages of rice growth when there is low flora and fauna composition.

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