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Microdam Impoundments Provide Suitable Habitat for Larvae of Malaria Vectors: An Observational Study in Western Kenya

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Abstract

Impoundments formed by microdams in rural areas of Africa are important sources of water for people, but they provide potential larval habitats for *Anopheles* (Diptera: Culicidae) mosquitoes that are vectors of malaria. To study this association, the perimeters of 31 microdam impoundments in western Kenya were sampled for *Anopheles* larvae in three zones (patches of floating and emergent vegetation, shorelines of open water, and aggregations of cattle hoofprints) across dry and rainy seasons. Of 3,169 larvae collected, most (86.8%) were collected in the rainy season. Of 2,403 larvae successfully reared to fourth instar or adult, nine species were identified; most (80.2%) were *Anopheles arabiensis* Patton, sampled from hoofprint zones in the rainy season. Other species collected were *Anopheles coustani* Laveran, *Anopheles gambiae* s.s. Giles, *Anopheles funestus* Giles, and *Anopheles rivulorum* Leeson, *Anopheles pharoensis* Theobald, *Anopheles squamosus* Theobald, *Anopheles rufipes* (Gough), and *Anopheles ardensis* (Theobald). Larvae of *An. funestus* were uncommon (1.5%) in both dry and rainy seasons and were confined to vegetated zones, suggesting that microdam impoundments are not primary habitats for this important vector species, although microdams may provide a dry season refuge habitat for malaria vectors, contributing to population persistence through the dry season. In this study, microdam impoundments clearly provided habitat for the malaria vector *An. arabiensis* in the rainy season, most of which was within the shallow apron side of the impoundments where people brought cattle for watering, resulting in compacted soil with aggregations of water-filled hoofprints. This observation suggests a potential conflict between public health concerns about malaria and people's need for stable and reliable sources of water.

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Authors' Contributions

R.M. and E.W. conceived the study. All authors contributed to the design of the study. R.M. and N.B. managed the field data collection. R.M. performed the statistical analysis and drafted the manuscript. All authors participated in the preparation of the manuscript, and read and approved the final manuscript.

Keywords

hydrology; immature insects; malaria; public health entomology; survey

Malaria transmission is intricately linked with water due to the obligate aquatic life stage of all malaria vector mosquito species. Still, the specific ecology of local malaria vectors determines which types of water bodies contribute to malaria transmission in a region (McKeon et al. 2013, Smith et al. 2013). While factors such as adult stage dispersal (Carter et al. 2000), host preference (Garrett-Jones 1964), and survival (Macdonald 1957, Smith et al. 2007) determine a malaria vector population's capacity to transmit malaria, identification of the specific aquatic habitat types used by malaria vector immature stages is critical for understanding malaria vector population dynamics across space and time (Killeen et al. 2004).

Infrastructure designed to manipulate the flow and retention of water, such as an irrigation scheme or dam, is generally designed to meet societal needs for reliable sources of water for domestic or agricultural use. Effects leading to increased malaria vector populations and thus effects on malaria transmission are not usually considered in the design of such infrastructure, and therefore the potential for increased malaria transmission exists (Keiser et al. 2005, Kibret et al. 2017). In Ethiopia, children living in close proximity to irrigation system microdams had an increased risk of malaria incidence compared to children living 8–10 km from microdams (Ghebreyesus et al. 1999), but environmental management of such habitats has shown potential for reducing this risk (Yohannes et al. 2005). Additionally, when the ecology of the local malaria vector is well understood, it may be exploited by specific water management techniques such as removing vegetation or fluctuating water levels to make the available standing water less suitable for the larvae (Kitron and Spielman 1989).

Microdams (Kiswahili: *ndiva*) in the east African setting are earthen, water harvesting structures of modest size that allow water storage through surface impoundment (Nicol et al. 2015). In western Kenya, earthen microdams are commonly built to impound water for use in small-scale irrigation, watering livestock, and domestic activities (Fig. 1). An up-to-date database of the microdams in Kenya does not exist, but around 50,000 microdams were constructed in Nyanza Province in western Kenya over 3 years in the 1950s (Hunter et al. 1982), with some still in use, and new microdams being built to date. These microdams are typically built in valleys, taking advantage of the natural drainage of water into each site, as opposed to damming a river or stream. The microdam structure itself is generally only a few meters high and may impound anywhere from approximately 100 m^3 to 500,000 m^3 of water, falling well under the definition of a large dam given by the International Commission on Large Dams (ICOLD 2011). The depth of the impounded water normally increases from only a few centimeters at the "upstream" edges to a meter or more at the "downstream" edge near the earthen microdam itself.

Despite the potential for small dams to provide suitable habitat for larval stages of *Anopheles* mosquito vectors of malaria (Jewsbury and Imevbore 1988), the effects of these dams on malaria in Africa have not been widely studied (Keiser et al. 2005). In western

Kenya, the extent of colonization of aquatic habitats along the perimeters of microdam impoundments by malaria vectors has not been previously investigated. Therefore, the objective of this study was to quantify malaria vector species use of aquatic habitats along microdam impoundment perimeters and characterize the overall anopheline community in the impoundment perimeters. Furthermore, we assessed the contributions of environmental conditions and seasonal differences in rainfall to variation in the *Anopheles* communities within microdam impoundments.

Materials and Methods

Study Site

This study took place in Asembo, a rural community of 79 villages in western Kenya (Siaya County). The region sits in the subhumid agro-ecological zone (Sombroek et al. 1982) in the lowlands along the shores of Lake Victoria, with elevations ranging from 1,100 m to 1,400 m above sea level and low topographic relief. The region is relatively densely populated, with about 60,000 residents living in an area of 200 km^2, and the landscape is dominated by agriculture. The majority of residents are subsistence farmers, primarily growing maize, sorghum, cassava, millet, or vegetables, and raising cattle, goats, or chickens (Phillips-Howard et al. 2003). Cattle are an important resource in the community, being used primarily for plowing fields and as an economic investment in addition to sources of dairy and meat products.

Rainfall in Asembo is seasonally bimodal with peaks usually occurring in October–November and March–May. However, rainfall may occur year-round, with monthly precipitation totals ranging from 7 to 490 mm and yearly totals ranging from 1,100 to 1,800 mm from 2003 through 2012. Mean daily temperatures range from 18 to 29°C. Malaria is holoendemic in the region, with parasitemia rates in children under five being around 50% in 2009 (Hamel et al. 2011). The predominant malaria parasite species is *Plasmodium falciparum* (Welch). The primary malaria vectors in the region are *Anopheles arabiensis* Patton, *Anopheles gambiae* s.s. Giles, and *Anopheles funestus* Giles. Other species of *Anopheles* known to occur in the region include *Anopheles coustani* Laveran, *Anopheles rufipes* (Gough), *Anopheles pharoensis* Theobald, and *Anopheles squamosus* Theobald. None of these species are known to transmit malaria parasites in western Kenya, although some have been reported as locally important malaria vectors in other regions of Africa (Carrara et al. 1990, Mwangangi et al. 2013, Stevenson et al. 2016).

Networks of streams run across the region and drain into Lake Victoria. Microdams in Asembo are constructed along these drainage basins. Impoundments created by microdams in this region are a primary source of water for livestock and for domestic use, including drinking water (Crump et al. 2005). The impoundments fill with rainwater during the two rainy seasons and are used by local residents throughout the year.

Seventy-two functional microdams were identified within Asembo by local residents for the current study, 24 of which had been built or renovated since 2000. Three of these were excluded from our study because they were located in a village where larvicide was being applied to *Anopheles* larval habitats, including microdam impoundments. Eighteen microdams were excluded because they were within 1 km of villages where insecticide-treated wall lining was applied to every house as part of a separate, controlled study. Of the remaining 51 microdams in Asembo, 31 still held water in February 2012 and were included in the current study.

Larvae Sampling

Microdam impoundments were sampled for *Anopheles* larvae in the first dry season and the first rainy season of 2012. Each microdam impoundment was sampled on 1 day from 3 through 22 February 2012 (dry season) and once from 30 April through 23 May 2012 (rainy season). Standardized samples were taken along the perimeter of each microdam impoundment at 20 m intervals. Each sample was taken from a quadrat measuring 2 m along the perimeter and 1 m into the impoundment and consisted of 20 300 ml dips taken at 20 s intervals. If sampling locations were primarily aggregations of hoofprints, dipping was considered impractical, and all larvae within the 2 by 1 m quadrat were collected using plastic pipettes (Mutuku et al. 2006). All collected larvae were kept in separate containers for each instar and sampling location. The larvae were reared in the lab to the fourth instar and identified to species according to Gillies and Coetzee (1987). In some cases, the larvae pupated prior to identification and were then reared to adults, which were also identified to species according to Gillies and Coetzee (1987). Specimens identified morphologically as part of the *An. gambiae* species complex were further differentiated to the species level by PCR (Scott et al. 1993). *An. funestus* species group larvae were identified to species with the method of Koekemoer et al. (2002). We did not differentiate between *An. pharoensis* larvae and *An. squamosus* larvae.

The habitat type for each sample was classified as either vegetated (when the sampling quadrat included patches of any floating and/or emergent vegetation), open water, or aggregations of hoofprints. These three habitat types were common among microdam impoundments, but the proportion of each varied. The percent vegetated habitat for each microdam was determined by calculating the proportion of samples classified as vegetated. The soil type for each microdam was determined using the 1:1,000,000 exploratory soil map of Kenya, compiled by the Kenya Soil Survey in 1980 (Sombroek et al. 1982). The three soil types were 1) friable clay/sandy clay loam, 2) friable clay, and 3) firm, silty clay/clay. Of these soil types, friable clay drains more quickly, and firm, silty clay/clay drains more slowly. Daily precipitation totals for December 2011 through May 2012, as measured by the weather station at the Kisumu Airport (about 40 km east of Asembo), were downloaded from the National Climatic Data Center's Global Summary of Day (GSoD) database.

Statistical Analyses

All analyses were performed separately for each season. To assess differences in the number of anopheline larvae per sample among habitat types (i.e., hoofprints, open or vegetated), we used general linear mixed models with a compound symmetrical correlation structure to account for repeated measures within microdam impoundments (i.e., multiple samples along the perimeter of each microdam impoundment). Separate analyses were performed for each malaria vector species and for the most abundant nonvector species. We also assessed the effects of microdam characteristics (i.e., the percentage of the habitat which had floating and emergent vegetation, and the soil type) on *Anopheles* species richness and larval density within microdam impoundments. Species richness was defined as the number of species observed in each microdam impoundment (Ricklefs and Relyea 2014). Larval density was calculated as the number of larvae collected per meter of impoundment perimeter sampled. We assessed the effect of the percentage of vegetated habitat and the soil type within microdam impoundments on larval density using general linear models with a separate analysis for each species. The association of *Anopheles* species richness to the percentage of vegetated habitat and the soil type was also assessed using a general linear model.

Results

Overall, 3,169 *Anopheles* larvae from nine species were collected. The species encountered were *An. arabiensis*, *An. gambiae* s.s., *An. pharoensis, An. squamosus, An. rufipes, An. coustani, An. funestus, Anopheles rivulorum* Leeson, and *Anopheles ardensis* (Theobald). In total, 980 *An. gambiae* s.l. was identified to species by PCR, 96% of which were *An. arabiensis*. For the *An. funestus* species group, 11 larvae were identified by PCR (10 *An. funestus* s.s. and 1 *An. rivulorum). Anopheles* species richness ranged from 0 to 6 species per microdam.

As expected, there was a dramatic difference in rainfall between the dry and rainy season sampling periods, both in the weeks preceding the sampling periods and during the sampling periods (Fig. 2). There were marked differences between dry and rainy season samples in the number of *Anopheles* larvae collected from microdam impoundments (Table 1). In the dry season, 419 *Anopheles* larvae were collected, 85% of which were identified to species. The primary reason for not being able to identify a specimen was death as an early instar or pupa. The most abundant species in the dry season was *An. pharoensis/squamosus* (52% of total collected). The life stages of collected specimens were not recorded in the dry season. In the rainy season, 2,750 *Anopheles* larvae were collected (75% identified to species), most of which were *An. gambiae* s.l. Of the specimens identified to species in the rainy season, 70% were either third instar, fourth instar, or pupae at the time of collection (Table 2).

The perimeters of the microdam impoundments also changed between seasons. While the water level in many of the impoundments remained relatively unchanged, the water level in some of the impoundments changed dramatically. The average length of the perimeter increased slightly from the dry season (mean, 168 m; range, 60–540 m) to the rainy season (mean, 183 m; range, 60–580 m). Changes in impoundment water level led to changes in the types of habitat occurring along the impoundment perimeter. Open water was the most common habitat type in the dry season, but vegetated habitat was more common in the rainy season (Table 3).

Larval densities of the most common *Anopheles* species differed among habitat types. In the dry season, *An. pharoensis/squamosus* larvae were more common in samples taken from hoofprint aggregations and vegetated locations relative to open water, whereas *An. funestus* larvae were most common in vegetated locations (Fig. 3). *An. gambiae* s.l. larvae were found in all three habitat types at similar densities in the dry season. In the rainy season, *An. gambiae* s.l. larvae were most common in hoofprint aggregations and *An. pharoensis/*

squamosus larvae were most common in vegetated locations (Fig. 4). Comparisons among habitat types were not made for *An. funestus* in the rainy season because only three *An. funestus* larvae were collected.

Species richness of *Anopheles* larvae increased with increasing vegetation in both seasons, though the effect was stronger in the dry season (Fig. 5). Soil type was not associated with species richness. Table 4 shows the effects of the percentage of the perimeter with vegetation and soil type on the relative density of larvae in the microdam impoundments. Higher densities of *An. funestus* larvae were found with higher percent vegetation in the dry season, and they were lowest in the firm, silty clay/clay soil type. In both seasons, the relative density of *An. pharoensis/squamosus* larvae was associated with the percent vegetation and soil type of the microdam impoundments. Finally, densities of *An. gambiae* s.l. larvae in the rainy season were higher in microdam impoundments with a lower percentage of vegetation.

Discussion

Anopheles larvae, including malaria vectors, used aquatic habitats along the edges of microdam impoundments in this study. *An. gambiae* s.l. larvae (predominately *An. arabiensis*) were found in microdam impoundments in both the dry and rainy seasons. Notably, all the impoundments sampled in this study were permanent water bodies, in that the water persisted throughout the dry season. *An. arabiensis* and *An. gambiae* s.s. are known to use a range of aquatic habitat types across their distributions, with the primary requirement being standing, fresh water (Gillies and De Meillon 1968). In Kenya, both species are apparently habitat generalists as larvae, occupying both temporary and permanent aquatic habitats (Githeko et al. 1996, Minakawa et al. 1999, Gimnig et al. 2001, Fillinger et al. 2004, Mutuku et al. 2006, Imbahale et al. 2011), but this is the first study of which we are aware that clearly documents the presence of these species in microdam impoundments in Kenya.

Variations in the use of microdam impoundments by anopheline larvae were associated with the types of available habitat along microdam impoundment perimeters. These associations corresponded with previous findings about habitat preferences of anopheline larvae. Many *Anopheles* species, including *An. funestus, An. squamosus*, and *An. pharoensis*, are associated with emergent vegetation in larval habitats because it provides protection from predators (Gillies and De Meillon 1968, Gimnig et al. 2001) and serves as a substrate for periphyton, a potential food source for mosquito larvae (Merritt et al. 1992, Rejmánková et al. 2013). Accordingly, these species were found at higher densities in vegetated habitats. Additionally, species richness was higher in microdam impoundment perimeters with higher percent vegetation, suggesting that vegetated perimeters provide more ecological niches for *Anopheles* larvae.

In contrast, *An. gambiae* s.l. larvae are often found in habitats without vegetation (Gimnig et al. 2001). The absence of predators in the small, temporary aquatic habitats utilized by *An. gambiae* s.l. more than other anopheline species suggests a strategy of avoiding predators altogether (Munga et al. 2006, Warburg et al. 2011) rather than preferentially inhabiting water bodies with emergent vegetation. While all of the impoundments sampled in this study were permanent, and therefore likely harbored predators, there was clear habitat heterogeneity within the impoundments leading to varying biological communities among habitat types within the impoundments. Thus, *An. gambiae* s.l. larvae may have been able to exploit specific habitats within the impoundment perimeters, such as hoofprint aggregations, that did not contain predators.

In addition to the effects of vegetation, differences in soil type were associated with differences among microdams in the number of larvae found for some species. Soil type potentially influences the density of larvae in a microdam impoundment indirectly through its influence on microbial communities (Bossio et al. 1998). *Anopheles* larvae feed primarily on bacteria (Merritt et al. 1992) or algae (Kaufman et al. 2006), and variation in nutrient availability among soil types may lead to differences in microbial biomass, diversity, and community composition. Additionally, the microbial community may produce semiochemicals that provide oviposition cues for *Anopheles* females (Lindh et al. 2008). However, the roles of soil type and microbial community ecology in the habitat use of *Anopheles* mosquitoes are not yet fully understood.

Anopheles communities in the microdam impoundments varied considerably between seasons, and this variation was likely driven by a combination of factors, including the population dynamics of *Anopheles* species, the availability of other aquatic habitats, and catchment-scale hydrology. The seasonal variation of *An. funestus* and *An. gambiae* s.l. population sizes are well characterized in this region, generally correlating positively with lagged precipitation (Beier et al. 1990, Taylor et al. 1990, Odiere et al. 2007). Therefore, higher collections of these two taxa would have been expected in the rainy season compared to the dry season, if microdam habitats were used equally relative to other larval habitats on the landscape. The lower relative density of *An. funestus* larvae in the rainy season sampling suggests that other larval habitats are more important than microdam habitats for *An. funestus* during its yearly peak in population abundance. Nevertheless, microdam habitats are potentially important for sustaining *An. funestus* and other *Anopheles* species in the dry season. The number of potential *Anopheles* larval habitats on the landscape in this region decreases by as much as 90% in the dry season (Mutuku et al. 2009), making microdam impoundments some of the few water bodies available to *Anopheles* larvae in the dry season. Thus, habitats along the perimeters of microdam impoundments potentially represent dry season refuge, which anopheline populations use to persist when other aquatic habitats dry up.

The density of *An. gambiae* s.l. larvae was considerably higher in the rainy season than the dry season, suggesting that utilization of microdam impoundments by *An. gambiae* s.l. is driven, at least partially, by population dynamics, and that microdam impoundments provide habitat for this species complex in the rainy season. The upstream edges of microdam impoundments in this region, which are typically very shallow relative to the downstream edge near the earthen microdam, provide an entrance into the impoundment for cattle and other livestock to drink water. With the substrates typically found near microdam impoundments in this region, the livestock leave abundant hoofprints in the trampled soil along the shallow end of the impoundment perimeter, creating suitable habitat for *An. gambiae* s.l.

The exact mechanisms by which *An. gambiae* s.l. larvae enter microdam habitats remain unclear and should be studied further. Potentially, female anophelines may oviposit in microdam impoundments. Additionally, larvae may be aggregated in microdam impoundments during the rainy season when they are flushed from other aquatic habitats upstream in the catchment area (Gimnig et al. 2001, Paaijmans et al. 2007). Heavy rainfall (i.e., over 20 mm daily total) during the rainy season in this region flows across the landscape, and microdams are designed to collect water flowing along these catchments. Therefore, even if *An. gambiae* s.l. females do not oviposit in microdam habitats, these habitats may contribute to *An. gambiae* s.l. population dynamics through larvae completing at least part of their life time in them.

Further studies are also required to quantify the contribution of microdam habitats, relative to that of other habitats, to the population dynamics of *An. gambiae* s.l. in the region. A previous study in this region (but in a village without microdams nearby) found high variation in *An. gambiae* s.l. pupal density among larval habitat types, with burrow pits and stream bed pools being the most productive habitat types (Mutuku et al. 2006). They also found a low correlation between early instar larval density and the density of *An. gambiae* s.l. pupae within larval habitats, suggesting the former is a poor proxy for adult productivity (Mutuku et al. 2006). Future studies should, therefore, compare pupal densities in microdam impoundments with other nearby habitat types in both dry and rainy seasons to elucidate the potential benefits of implementing larval source management in microdam impoundments for malaria control.

The presence of *An. gambiae* s.l. as late instar larvae and pupae in microdam impoundments in the current study showed that microdams in western Kenya, which meet an important human demand for stable and reliable sources of water for both agricultural and domestic use, also provide suitable habitat for malaria vectors. Although further information is needed, the characteristics of microdams suggest larval source management would be a feasible malaria control strategy in these habitats. Microdams are few, fixed and findable, thereby fitting World Health Organization criteria for larval source management (World Health Organization 2013). Targeted larviciding at microdams during the dry season could slow the buildup of vector populations going into the rainy season. Additionally, using a different substrate to reduce livestock hoofprint aggregations, or some other type of habitat modification, could dramatically decrease the productivity of microdams in the rainy season.

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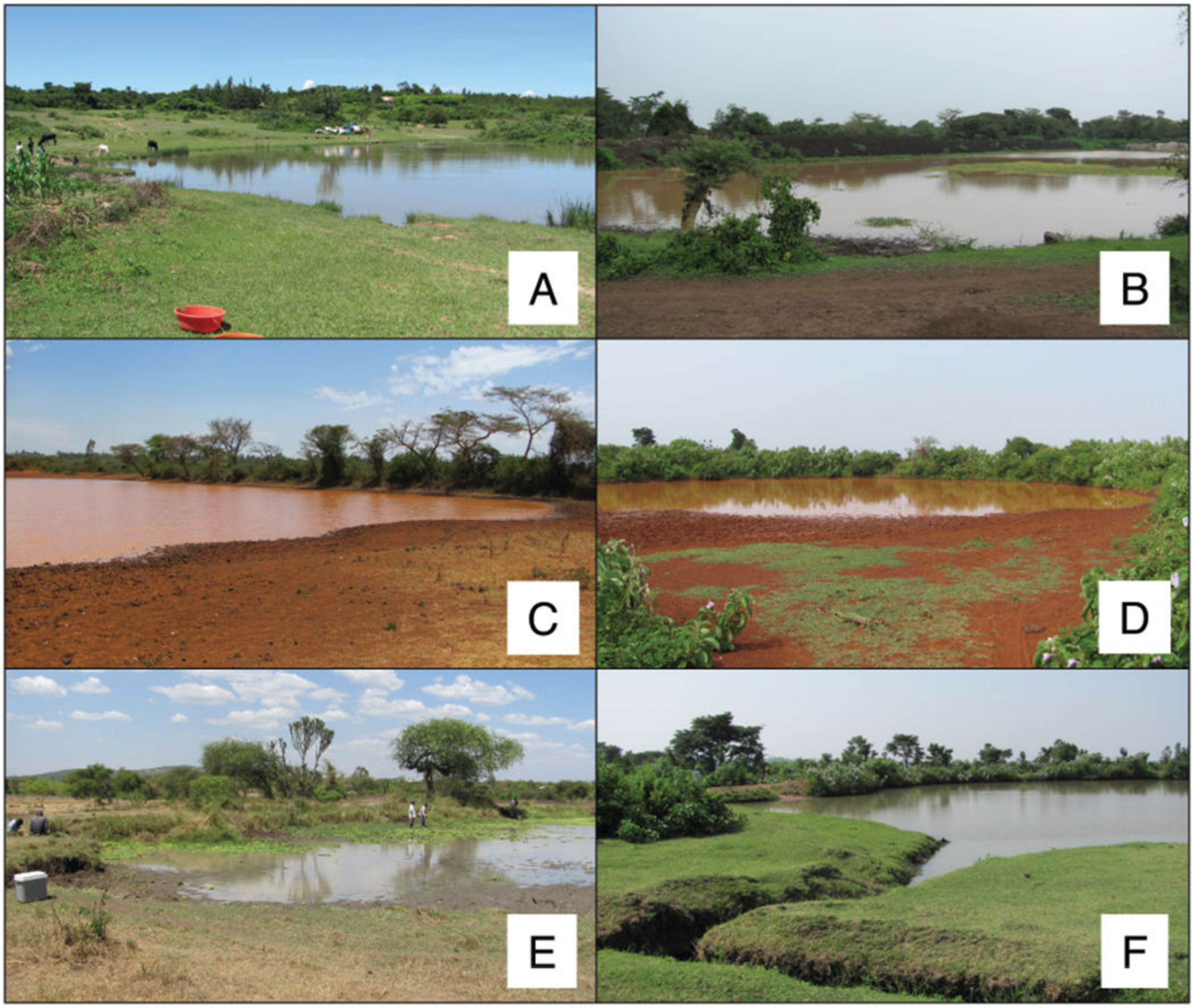

Fig. 1.

Six representative microdam impoundments that were sampled in this study. (A) Laundry tubs and cattle show multiple uses. (B) Vegetation-covered earthen dam in background, shallow soil apron in foreground, patches of floating vegetation. (C) Older microdam with acacia trees established on the earthen berm and bare, trampled soil. (D) Smaller impoundment with extensive cattle hoofprints and bicycle tracks indicate human visits. (E) Dry season photo showing receding water line, floating vegetation, and mud margins. (F) Wet season photo showing earthen microdam in background and dug channel for water inlet in foreground.

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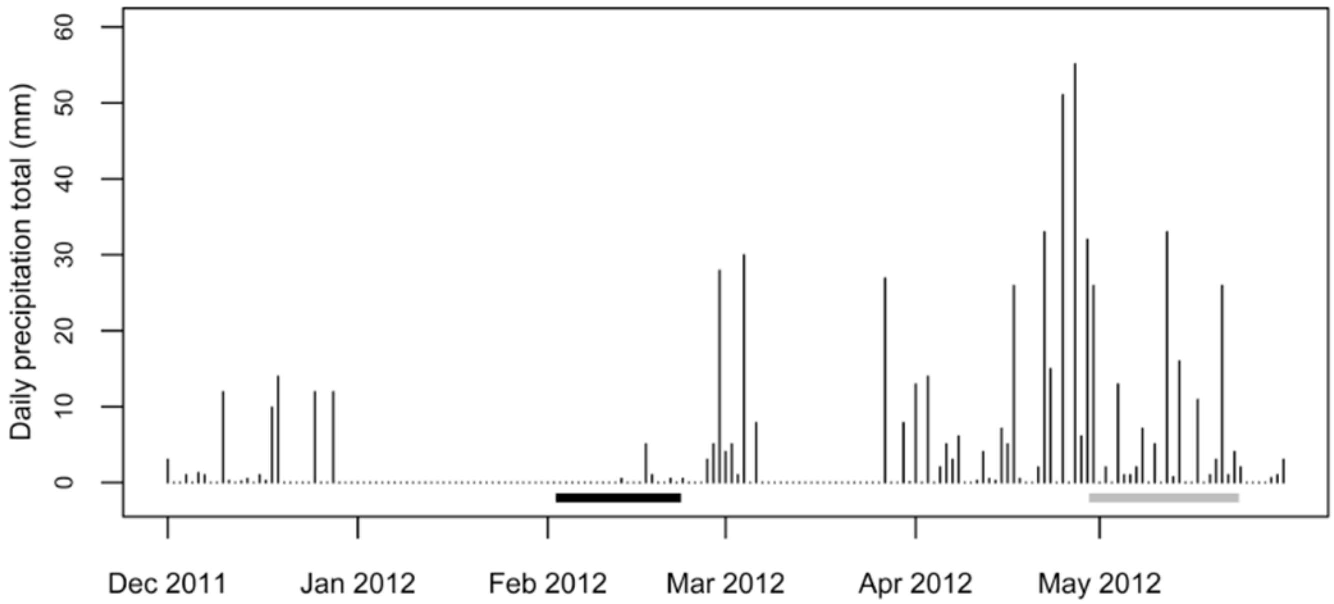

Fig. 2.
Daily precipitation totals (vertical bars) for 1 December 2011 through 31 May 2012. Horizontal black line indicates dry season period for *Anopheles* sampling from microdams, while the gray line indicates the rainy season sampling period.

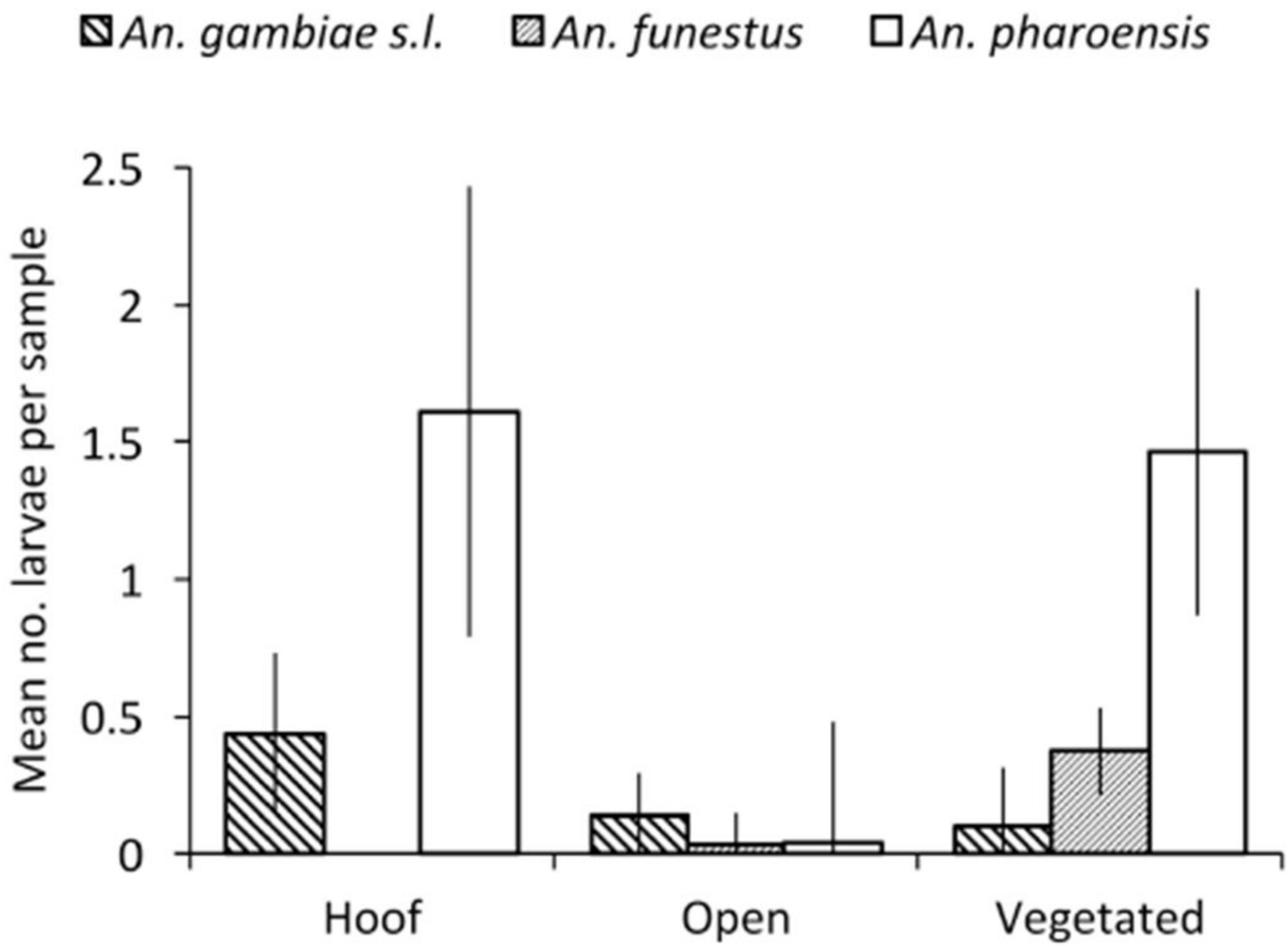

Fig. 3.
For the dry season, the mean number of *Anopheles* larvae per sample, by species, collected from three habitat types on the perimeters of microdams. Error bars are 95% confidence intervals. Results shown for *An. pharoensis* are for larvae identified as *An. pharoensis/ squamosus.*

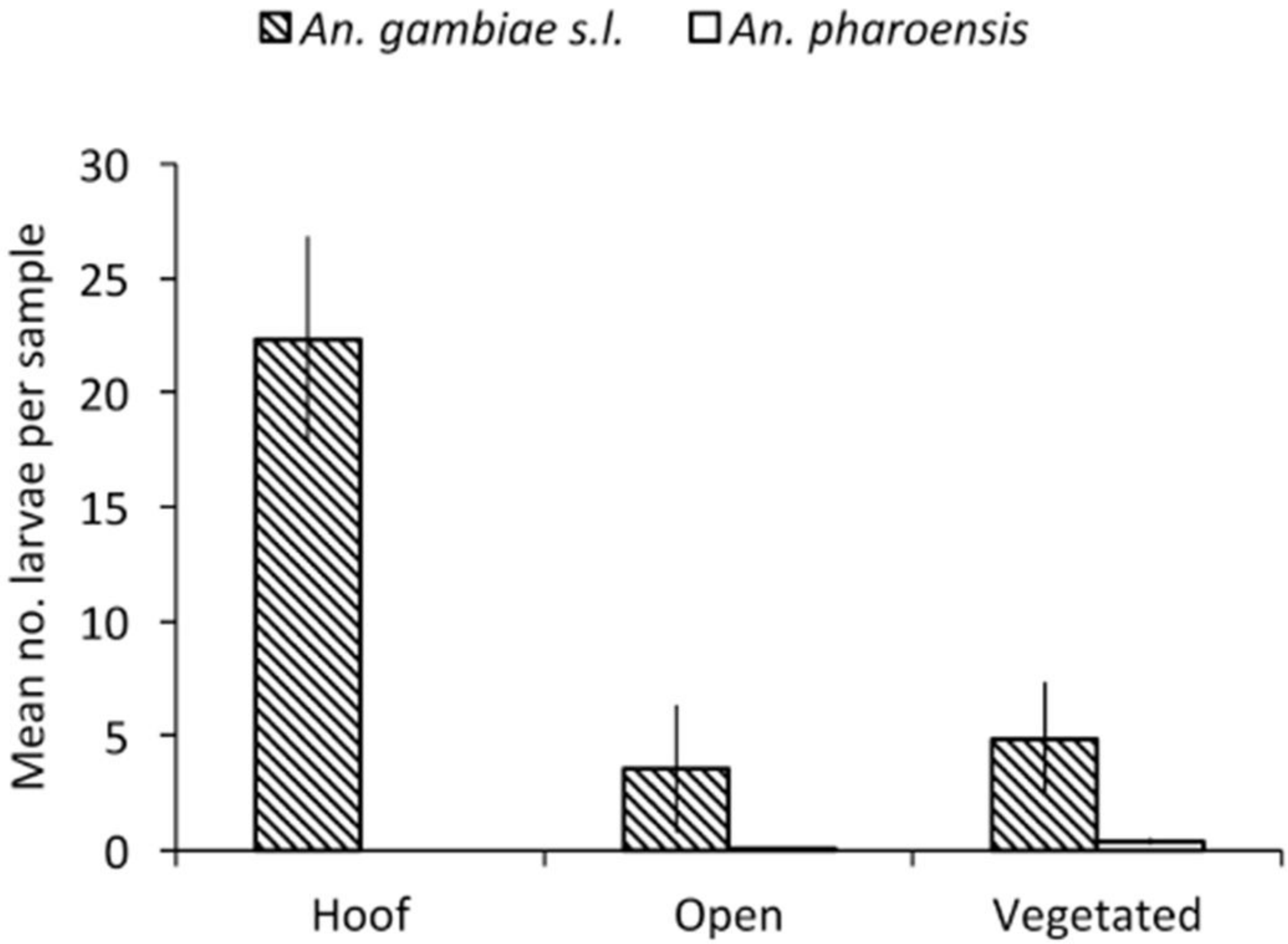

Fig. 4.

For the rainy season, the mean number of *Anopheles* larvae per sample, by species, collected from three habitat types on the perimeters of microdams. Error bars are 95% confidence intervals. Results shown for *An. pharoensis* are for larvae identified as *An. pharoensis/squamosus. An. funestus* are not shown for rainy season sampling because only three *An. funestus* larvae were collected.

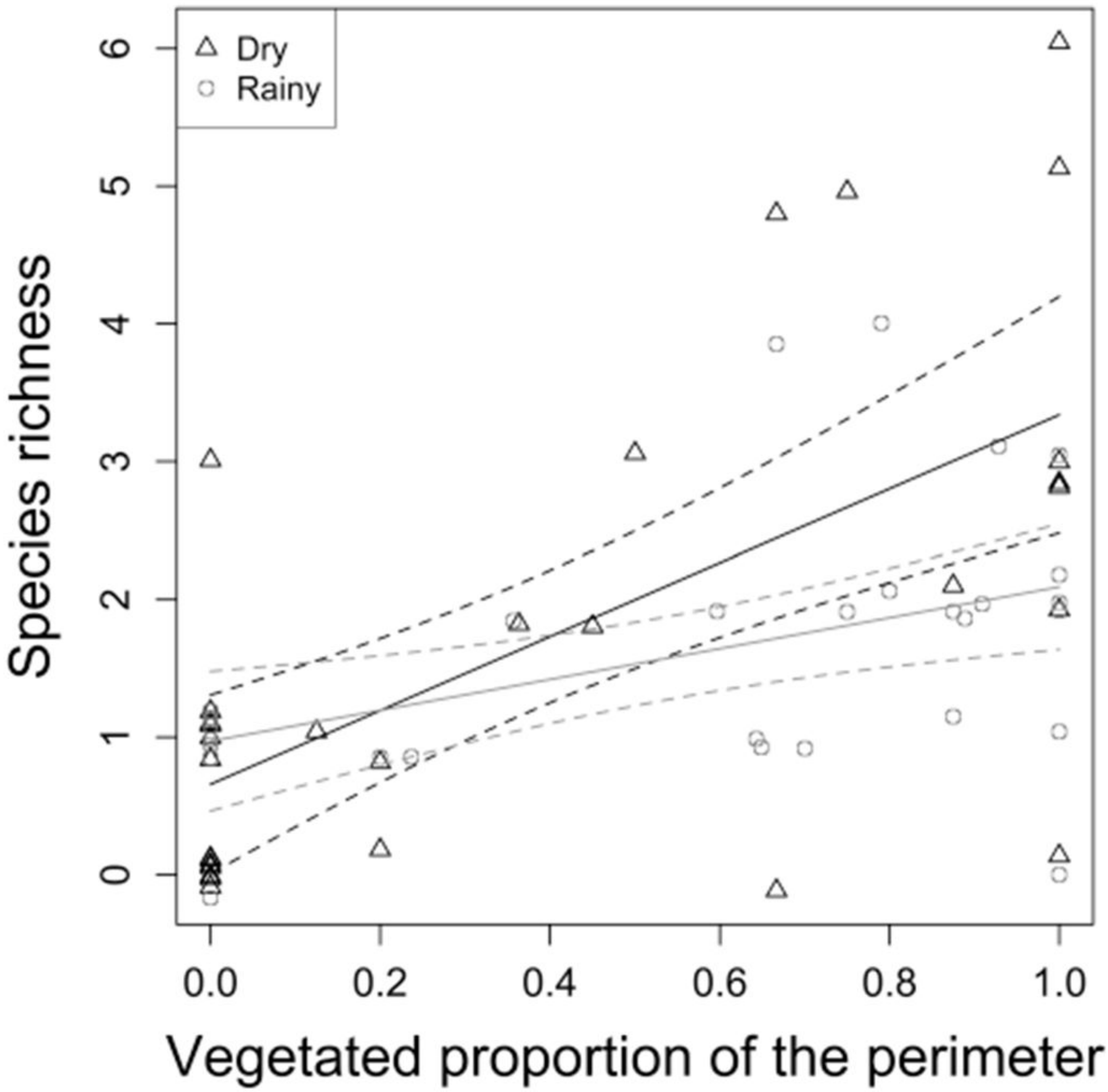

Fig. 5.

Dry and rainy season species richness of *Anopheles* larvae collected from microdam impoundment perimeters, by the percent of the perimeter that was vegetated. Points show observed data (n = 31 microdams per season), jittered along the y-axis to reduce plotting points over each other. Solid lines show estimates from separate linear regressions for the dry season (black) and the rainy season (gray), with broken lines showing 95% confidence intervals.

Table 1.

Number of larvae collected from the perimeters of microdam impoundments

Species	No. collected	
	Dry season (%)	Rainy season (%)
Anopheles gambiae s.l.	45 (12.6%)	1,963 (95.9%)
Anopheles pharoensis/squamosus	185 (52.0%)	55 (2.7%)
Anopheles rufipes	14 (3.9%)	17 (0.8%)
Anopheles coustani	53 (14.9%)	7 (0.3%)
Anopheles funestus	33 (9.3%)	3 (0.1%)
Anopheles ardensis	26 (7.3%)	2 (0.1%)

For each species of *Anopheles*, the percent of the total *Anopheles* identified in each season is shown in parentheses.

Table 2.

Number of immature mosquitoes collected in the rainy season by species and life stage at time of collection

Species	First instar (%)	Second instar (%)	Third instar (%)	Fourth instar (%)	Pupae (%)
Anopheles gambiae s.l.	309 (16%)	286 (15%)	385 (20%)	871 (44%)	112 (6%)
Anopheles pharoensis/squamosus	6 (11%)	13 (24%)	16 (29%)	17 (31%)	3 (5%)
Anopheles rufipes	0 (0%)	2 (12%)	8 (47%)	7 (41%)	0 (0%)
Anopheles coustani	1 (14%)	1 (14%)	3 (43%)	2 (29%)	0 (0%)
Anopheles funestus	0 (0%)	0 (0%)	2 (67%)	1 (33%)	0 (0%)
Anopheles ardensis	0 (0%)	1 (50%)	1 (50%)	0 (0%)	0 (0%)
Unidentified	208 (30%)	165 (23%)	162 (23%)	158 (22%)	10 (1%)

The percent shown in parentheses represents the number of that life stage out of the total collected for that species.

Table 3.

Number of samples taken for *Anopheles* larvae in the dry and rainy seasons of 2012 by habitat type

Habitat type	Dry	Rainy	Total
Hoofprint	41	41	82
Open water	140	106	246
Vegetated	78	137	215
Total	259	284	543

Table 4.

Effect of soil type and percent vegetation along the perimeter on the density of larvae collected per microdam

Species	Parameter	Dry season		Rainy season	
		Effect ± SE	*P*	Effect ± SE	*P*
Anopheles funestus	Percent vegetation	**0.26 ± 0.11**	**0.027**	NA	NA
	Soil type 1–2	−0.10 ± 0.09	0.310	NA	NA
	Soil type 1–3	**−0.26 ± 0.11**	**0.035**	NA	NA
Anopheles gambiae s.l.	Percent vegetation	−0.06 ± 0.10	0.526	**−4.08 ± 2.09**	**0.061**
	Soil type 1–2	−0.09 ± 0.08	0.289	1.24 ± 1.79	0.497
	Soil type 1–3	−0.08 ± 0.10	0.457	1.77 ± 2.21	0.431
Anopheles pharoensis/squamosus	Percent vegetation	**0.45 ± 0.25**	**0.083**	**0.19 ± 0.08**	**0.027**
	Soil type 1–2	−0.40 ± 0.22	0.073	−0.03 ± 0.07	0.643
	Soil type 1–3	**−0.57 ± 0.27**	**0.040**	**−0.15 ± 0.08**	**0.081**

Soil type 1, friable clay/sandy clay loam; soil type 2, friable clay; soil type 3, firm, silty clay/clay. Bold indicates $P < 0.10$. NA indicates not applicable because too few larvae were collected.