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Culex quinquefasciatus mosquito avoids ovipositing in habitats with the annual fish (*Nothobranchius neumanni*) in Tanzania

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Abstract Mosquitoes are known to choose oviposition habitats actively based on their suitability for survival of their offspring. They thus avoid laying eggs in dangerous habitats with aquatic predators through detection of their cues. Visual, tactile, and chemical cues emitted by certain predators have been shown to reduce oviposition in some mosquitoes, which in turn may affect their adult population sizes. However, those tests tend to be limited to species from temperate regions. Moreover, mosquito oviposition response to predator cues have been shown to be predator specific, but this has not been investigated for many potential predators worldwide. In the African subtropics, temporary ponds can be important mosquito breeding habitats and the same habitats are also used by a group of specialized killifish that can survive dry periods using drought resistant eggs. Although they are reported as mosquito predators, it is unknown whether mosquitoes actively avoid laying eggs in ponds with annual killifish. We investigated this using the mosquito *Culex quinquefasciatus* and the free and caged killifish *Nothobranchius neumanni* in the outdoor mesocosm experiments in Tanzania. We found that *Cx. quinquefasciatus* had 71% lower oviposition in mesocosms with free swimming killifish and 68% lower oviposition in mesocosms with caged killifish. We conclude that predator-released chemical cues alone are enough to explain the observed responses. If the cues can be isolated and chemically identified can be developed into a biological mosquito control strategy and used to safeguard public health in areas where mosquito borne diseases are endemic.

Keywords Habitat selection · Mosquito · Predator · Kairomone · Chemical cue · Mesocosm

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Introduction

Gravid female mosquitoes are known to actively choose suitable aquatic habitats to deposit their eggs in (Trekels and Vanschoenwinkel 2019). This strategy enables them to avoid ovipositing in dangerous habitats such as ponds with aquatic predators and thereby reduces the risk of their offspring mortality (Silberbush and Blaustein 2011). Avoiding oviposition in habitats with predators is one of the ways insects without parental care, including mosquitoes, can promote offspring survival (Eveland et al. 2016). They achieve this by detecting non-chemical cues (visual and tactile) as well as chemical cues (kairomones) released by predators into aquatic habitats using well-developed chemosensory receptors (Why and Walton 2020). Kairomones are information-carrying chemicals produced by an individual of one species (the donor: e.g., a predator) and received by an individual of a different species (the receiver: e.g., a prey), benefiting the receiver (which flee away or change shape) and often disadvantaging the donor (Silberbush et al. 2010). In mosquitoes, kairomonal responses have been demonstrated in several studies. For example, Ohba et al. (2012) showed that the gravid *Culex tritaeniorhynchus* mosquito laid fewer egg rafts in mesocosms with water conditioned by a single diving beetle *Eretes griseus* compared to mesocosms with dechlorinated tap water as a control.

However, evidence is accumulating that response of a specific gravid mosquito to kairomones from predators might be highly predator-specific and should not be generalized. For example, Silberbush et al. (2017) demonstrated that the number of egg rafts deposited by the gravid mosquito *Culex restuans* in control tubs containing tap water did not differ from that deposited in tubs containing two caged green sunfish *Lepomis cyanellus*, or pirate perch *Aphredoderus sayanus*. However, the same mosquito deposited two to three times more egg rafts in control tubs compared to tubs with two caged mosquitofish *G. affinis* as predators. Warburg et al. (2011) demonstrated that the synthetic hydrocarbons n-heneicosane (0.16 µg) and n-tricosane (0.97 µg) which mimic hydrocarbons extracted as chemical cues from *Notonecta maculata* conditioned water could not significantly reduce oviposition in certain *Anopheles gambiae* strains. Although they did not seem to affect this *Anopheles* strain, the same hydrocarbons were able to reduce oviposition by the gravid mosquito *Culiseta longiareolata* by 47% (n-heneicosane) and 58% (n-tricosane) (Silberbush et al. 2010). These studies indicate that predator-released kairomones influence oviposition patterns in mosquitoes which in turn may affect the burden associated with large biting mosquito population sizes. If the cues can be chemically identified as was done successfully for *N. maculata* (Silberbush et al. 2010), they may have direct use in the biological control of mosquitoes. However, the oviposition responses to the chemical cues of many candidate predators have not been tested for many important mosquitoes. Particularly relevant are the responses of mosquitoes of epidemiological importance.

Among all tested predators for mosquito larval control, fish are the commonly used in many countries (Chandra et al. 2008). Typical fish used for mosquito control include the mosquitofish *G. affinis* and the Guppy *Poecelia reticulata*. These fish have been translocated from their native ranges to reduce mosquito larvae, mainly in small permanent pond ecosystems. Since they cannot survive pond drying, they tend to be useless for mosquito control in temporary ponds, where many mosquitoes like to breed (Chandra et al. 2008; WHO 2013). African killifish from the genus *Nothobranchius* (Cyprinodontiformes) are peculiar fish that manage to survive pond drying using drought resistant eggs (Reichard et al. 2009). The first report of *Nothobranchius* killifish predation on mosquito larvae dates from 1941 from a laboratory experiment in which killifish *Nothobranchius taeniopygus* were shown to prefer mosquito larvae over other prey items (Vanderplank 1941). Later Matias and Adrias (2010) performed a mesocosm experiment in which the killifish *Nothobranchius guentheri* preferred to prey on larvae of *Cx. quinquefasciatus* over other prey (i.e., rotifers and chiromid larvae). These studies concluded that the tested *Nothobranchius* killifish which are indigenous to East Africa can be used as potential mosquito control agents in this region by introducing them (Vanderplank 1941), or their diapausing eggs (Matias and Adrias 2010) into temporary pools. However, Reichard and co-workers (2010) substantially criticized this conclusion. First, successful introduction of *Nothobranchius* fish into temporary ponds is limited by the presence of suitable substrate for survival of their eggs—the alluvial vertisol soil, without which eggs cannot survive drought. In the field not every temporary pond is on this soil. Second, according to the limited diet studies available, *Nothobranchius* fish are generalist predators with no strong preference to a particular prey, and mosquitoes are a rare component of their diet (Polačik and Reichard 2010). Although Reichard and co-workers (2010) were right, they neglected one major aspect that killifish could have negative effect on mosquito populations without predation when prospective gravid females avoid laying eggs in habitats where killifish reside. Such responses to fish are known in mosquitoes (Trekels and Vanschoenwinkel 2019; Why et al. 2016) but have never been tested in killifish and the consequences of this for biocontrol of mosquitoes have not been explored.

This study therefore was conducted to test the oviposition response of the tropical *Cx. quinquefasciatus* mosquito to the presence of the endemic killifish *Nothobranchius neumanni* (Hilgendorf, 1905) in Tanzania using field mesocosm experiments. We specifically intended to: (1) test the oviposition response of *Cx. quinquefasciatus* mosquito to the presence of the free-swimming killifish, and (2) test the oviposition response of *Cx. quinquefasciatus* mosquito to the presence of the caged killifish. The free-swimming fish is expected to emit both visual, olfactory, and tactile cues that might be detected by ovipositing mosquitoes, while the main cues provided by the caged fish will be olfactory. However, visual cues were not expected to be important in this study as mosquito oviposition typically happens at night (Why et al. 2016). Since some mosquito species have been shown to avoid oviposition in habitats containing predators (Table 1), we hypothesized (H_1) that presence of the predator killifish *N. neumanni* in oviposition habitats will also deter *Cx. quinquefasciatus* oviposition. Two experiments were performed. The first experiment tested oviposition response of *Cx. quinquefasciatus* mosquito to the presence of free-swimming killifish, and afterwards the second experiment was performed to test the same mosquito response to the caged killifish.

Materials and methods

Study area

The study was conducted in the village of Magugu in Babati district in Tanzania at the Tropical Pesticide Research Institute (TPRI) field center (UTM 36 M: 808,649; 9,557,041; elevation: 1004 m asl). The area is characterized by an average daily temperature of 19.4 °C (Nyembo et al. 2021) and two rainy seasons with an average annual precipitation of 690 mm (Nonga et al. 2011). Short rains fall from November to January and long rains from March to May. Common mosquito species present in the village are *Cx. quinquefasciatus, Culex unnivittatus, Anopheles arabiensis, Anopheles pharoensis, Anopheles coustani, Anopheles funestus, Anopheles marshallii, Anopheles maculpalpis* (Mwanziva et al. 2011) and *Aedes aegypti* (Mataba et al. 2022), and their abundances increase during the rainy season (Mwanziva et al. 2011).

Experimental design

Two field mesocosm experiments were conducted. The first experiment was a 10-day experiment that ran from 2nd–11th December 2020 and comprised of two (2) treatments (control tanks, and tanks with caged *N. neumanni* killifish) each with six replicates (Table S3). Twelve (12) green plastic tubs (150lts) (diameter:120 cm, height:60 cm) (Fig. 1b) were arrayed in a 70 m x 60 m field with a homogenous flat topography, with spatial placement of mesocosms following a complete randomized 'Latin square' design. To promote independency of the mesocosms, the mesocosms were placed 10 m apart. Ninety (90) liters of dechlorinated tape water were added to each mesocosm followed by 10 mg of rabbit chow pellets (Harsho Milling Co. Ltd, Kilimanjaro, Tanzania). Rabbit chow supplied nutrients and organic matter as a food source for mosquitoes (dead organic matter and associated biofilms). To allow initial decomposition of organic substances (rabbit chow), and to prevent immediate mosquito colonization during this process, mesocosms were covered by mosquito nets (1.2 mm mesh size) and left closed for four (4) days. Two days prior to the start of the experiment a single cage was inserted in each mesocosm including the six control mesocosms followed by addition

Table 1 List of mosquito species that have been experimentally confirmed to show reduced oviposition in pools containing the listed predators

Sn	Predator	Mosquito	Oviposition reduction (%)	Location	References
1	Fish *Gambusia affinis* (conditioned water)	*Culex restuans*	84	Washington, USA	Eveland et al. (2016)
2	Fish *Gambusia affinis* (conditioned water)	*Culex tarsalis*	71	California, USA	van Dam and Walton (2008)
3	Fish *Gambusia affinis* (conditioned water)	*Culex quinquefasciatus*	27	California, USA	van Dam and Walton (2008)
4	Fish *Gambusia affinis* (conditioned water)	*Culex pipiens* complex	69	North Carolina, USA	Angelon and Petranka (2002)
5	Caged fish *Gambusia affinis*	*Culex pipiens* and *Culex laticinctus*	75	Tivon, Israel	Cohen and Silberbush (2021)
6	Caged fish *Gambusia affinis*	*Culiseta longiareolata*	29	Tivon, Israel	Silberbush (2021)
7	Caged Aphanius mento	*Culiseta longiareolata*	23	Tivon, Israel	Silberbush (2021)
8	Caged fish *Lepomis gibossus*	*Culex pipiens*	91	Brussel, Belgium	Trekels and Vanschoenwinkel (2019)
9	Fish *Melanotaenia duboulayi* (conditioned water)	*Culex Annulirostris*	83	Queensland, Australia	Hurst et al. (2010)
10	Caged fish *Lepomis macrochirus*	*Anopheles punctipennis*	80	North Carolina, USA	Petranka and Fakhoury (1991)
11	Caged fish *Epiplatys spilargyreius*	Culicines (*Culex* and *Aedes*)	97	Farafenni, Gambia	Louca et al. (2009)
12	Caged fish *Tilapia guineensis*	Culicines (*Culex* and *Aedes*)	93	Farafenni, Gambia	Louca et al. (2009)
13	Fish *Gila orcutti* (conditioned water)	*Culex tarsalis*	72	California, USA	Why et al. (2016)
14	Caged newt *Notophthalmus viridescens louisianensis*	*Culex restuans*	29	Washington, USA	Eveland et al. (2016)
15	Free and caged *Notonecta irrorata*	*Culex restuans* and *Culex pipiens*	77	Washington, USA	Blaustein et al. (2005)
16	Free *Notonecta maculata*	*Culiseta langiareolata*	64	Israel	Eitam and Blaustein (2004)
17	Free *Notonecta maculata*	*Culex laticinctus*	78	Israel	Blaustein et al. (2003)
18	Free *Anisops sardea*	*Culiseta longiareolata*	87	Israel	Eitam et al. (2002)
19	Free *Anax imperataor*	*Culiseta longiareolata*	63	Israel	Stav et al. (2000)
20	Beetle *Eretes griseus* (conditioned water)	*Culex tritaeniorhynchus*	87	Nagasaki, Japan	Ohba et al. (2012)
21	Free *Notonecta glauca*	*Culex pipiens*	75	Belgium	Santangelo et al. (2021)
22	Free *Cordulia aenea* and *Aeshna cyanea*	*Culex pipiens*	92	Belgium	Santangelo et al. (2021)

of two killifish predators in treatment mesocosms (TL:8–12 cm). Each cage (Fig. 1a) was a 20lts non-transparent green plastic bucket (diameter:40 cm, height:60 cm) perforated on all sides including the lid (40 holes; diameter: 0.8 cm) to allow exchange of fish exudates between the inside and outside of the cage. We also confirmed that fish in the cages were not visible to the mosquitoes through the perforations as the inside of the cages was dark, which obscured the fishes. The experiment started on the 2nd of December 2020 when netting was removed to allow for mosquito oviposition and ended on the11th of December 2020. Fish were kept alive by feeding them with four Chironomidae larvae (bloodworm fish food) added to

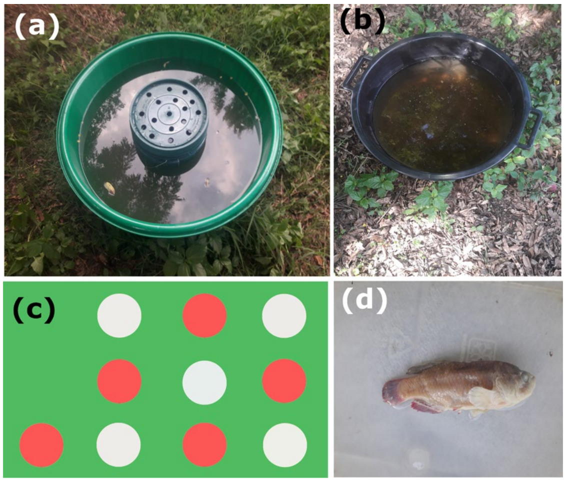

Fig. 1 Mesocosms and a predator cage used in field experiments that tested oviposition habitat selection of the mosquito *Culex quinquefascatus* in response to the killifish *Nothobranchius neumanni*. **a** Mesocosms with inserted cage used in the first experiment with caged *N. neumanni* killifish predators. **b** Mesocosms used in the second experiment with a free-swimming *N. neumanni* killifish predator. **c** Spatial placement of mesocosms in the field, red cycles are mesocosms with *N. neumanni* killifish and non-red cycles are mesocosms without *N. neumanni* killifish. **d** *N. neumanni* killifish that was used in these experiments

each mesocosm each day including the control mesocosms. Colonizing adult insects (e.g., water beetles) were removed when detected. To avoid overflow of mesocosms during rains drainage holes were drilled just above the original water line. Nearby vegetation, dwellings, and other structures served as a source of ovipositing mosquitoes. *Culex* mosquitoes deposit eggs on the water surface in floating rafts that are visible to the naked eye, each containing 100–300 eggs (CDC 2020). Every 24 h at 8:30 in the morning *Culex* egg rafts were visually counted on the water surface of each mesocosm and removed using a 0.01-mm mesh aquarium net. Since the deposition of each raft is the result of a single decision, counts of the number of rafts are typically used as a measure of oviposition site selection (Trekels and Vanschoenwinkel 2019). Therefore, each egg raft was considered as one oviposition event. Some egg rafts were collected, allowed to hatch in a spare mesocosm and larvae allowed to grow to fourth instar and identified to species level with the aid of a dissecting microscope (Optika, magnification 40x) and dichotomous identification keys from Harbach (1985) for *Culex Dutton*; Snell (2005), Azari-Hamidian and Harbach (2009), and Harbach (1985) for *Cx. quinquefasciatus*, and Devi and Singh (2018) for *Lutzia tigripes* mosquitoes. Planktonic algal and cyanobacterial growth were estimated at the same time when egg rafts were counted as concentrations of chlorophyll-a and phycocyanin which were daily measured in situ in each mesocosm using a portable fluorometer (AquaFluoro-Tuner designs, Model 8000–010, USA). The experimental site had shade from trees that were sparsely distributed across the entire experimental site. However, the randomized position of mesocosms on the site ensured that variation in shade was evenly distributed over the treatments. This eliminated the possibility of shade and ambient temperature to act as confounding variables and bias results. Abiotic conditions, i.e., pH, temperature (°C), conductivity (µs/cm), salinity (PSU), and total dissolved solids (TDS) (mg/l) were not measured due to a malfunctioning instrument-the multiparameter meter.

In a second experiment, we tested to what extent a free-swimming killifish may reduce mosquito oviposition. This 10-day experiment ran from 12 to 21st December 2020. The set up for this experiment was similar to the first experiment except for few modifications (Table S6). The used mesocosms were 60 l black tubs (diameter:25 cm, hight:25 cm) with no inserted cages (Fig. 1c). Twenty (20) liters of dechlorinated tape water were added in each mesocosm, and one free swimming killifish predator was added as a treatment in six mesocosms.

Data analysis

Data from the two experiments were analyzed and figures plotted using R software version 3.6.2 (R Core Team 2019) and packages stats, MASS, lme4, multcomp, and ggplot2. Data were log-transformed when this helped to meet assumptions of normality or homoscedasticity. Variation in mosquito oviposition between treatments was analyzed per day and cumulatively for the entire duration of the experiment (with all deposited egg rafts pooled per treatment). A generalized linear model with a negative binomial error distribution was used to analyze differences in the number of egg rafts between treatments on each day and over the entire duration of the experiment. Variation in the number of egg rafts between days for each treatment was evaluated using a generalized linear mixed model with a negative binomial error distribution (as is suitable for count data) with day specified as a continuous fixed factor, mesocosm as a random factor and number of deposited egg rafts as a response variable. The negative binomial error distribution was used instead of the Poisson distribution because overdispersion was observed in the fitted values. Overdispersion in fitted values was determined when the ratio of residual deviance over residual degrees of freedom was greater than one in a Poisson distribution. Variation in the concentration of chlorophyll-a between treatments on each day and over the whole duration of the experiment was evaluated using generalized linear model with Gamma error distribution. Variation in the concentration of chlorophyll-a between days for each treatment was evaluated using a generalized linear mixed model with Gamma error distribution with date specified as a fixed factor, mesocosm as a random factor and chlorophyll-a as a response variable. To evaluate if the trophic state of the mesocosm influenced oviposition we applied a generalized linear mixed model with a negative binomial error distribution with chlorophyll-a and treatment specified as fixed factors, mesocosm as a random factor and number of egg rafts as a response variable. Four mesocosms were removed from analysis because they were stolen during caged killifish experiment. One control mesocosm was stolen on the second day of the experiment, two killifish mesocosms on the fifth day, and one killifish mesocosm on the sixth day.

Results

Mosquitoes that oviposited in the mesocosms were *Cx. quinquefasciatus*, *Cx. duttoni* and *L. tigripes*. *Culex quinquefasciatus* accounted for most of the oviposition (96%) while oviposition by *Cx. duttoni* and L. *tigripes* were rare.

Experiment 1: Caged killifish

A total of 1621 *Culex* egg rafts were collected. The mean number of egg rafts over the whole duration of the experiment was 68% lower in the caged killifish treatment than in the control ($\chi^2 = 14.28$, df = 1, $P = 0.0002$, Fig. 2a, Table 2). This pattern was also observed on each day of the experiment (all $P < 0.05$), except on the third, fourth and sixth day when the same trend was observed but it was not significant (Fig. 2b, Table S1). There was no significant variation in the mean number of egg rafts between days (Fig. 2b).

Chlorophyll-a concentrations were not significantly different between treatments over the duration of the experiment ($\chi^2 = 0.14$, df = 1, $P = 0.71$, Fig. 2c, Table 2) nor on individual days of the experiment (all $P > 0.005$, Table S2). Variation in the concentration of chlorophyll-a between days in the caged killifish treatment was not significant. However, in the control treatment concentration of chlorophyll-a differed significantly between days ($P < 0.05$), where it was lower on the 1st day than on the 4th, 5th, 6th, 7th, 8th, 9th, and 10th day of the experiment (Fig. 2d). It was also lower on the 2nd than on the 9th, and 10th day of the experiment. Further analyses of variation in the concentration of phycocyanin was dropped because levels of chlorophyll-a and phycocyanin were highly correlated (r = 0.91, t = 7.04, df = 10, $P < 0.001$). The predictive model showed that number of deposited egg rafts was negatively affected by the caged killifish ($\chi^2 = 8.52$, df = 1, $P = 0.0035$) and increasing concentration of chlorophyll-a ($\chi^2 = 12.69$, df = 1, $P = 0.00037$, Table 3).

Experiment 2: Free swimming killifish

A total of 544 *Culex* egg rafts were collected. The mean number of egg rafts deposited over the entire duration of the experiment was 71% lower in the free killifish treatment than in the control ($\chi^2 = 65.24$, df = 1, $P < 0.001$, Fig. 3a, Table 2). The same significant difference was maintained on each day of the experiment (all $P < 0.005$) except on day six (6), when the same trend was observed but was not significant (Fig. 3b). The number of deposited egg rafts did not vary between days in either treatment (Fig. 3b, Table S4).

There was no significant difference in the mean concentration of chlorophyll-a between treatments over the entire duration of the experiment ($\chi^2 = 3.35$, df = 1, $P = 0.067$, Fig. 3c, Table 2). This trend was maintained on each day (all $P > 0.05$) except on the first and second days of the experiment, when chlorophyll-a was higher in the control than in the free killifish treatment (all $P < 0.05$, Fig. 3d). Also, chlorophyll-a was higher in the first and second day

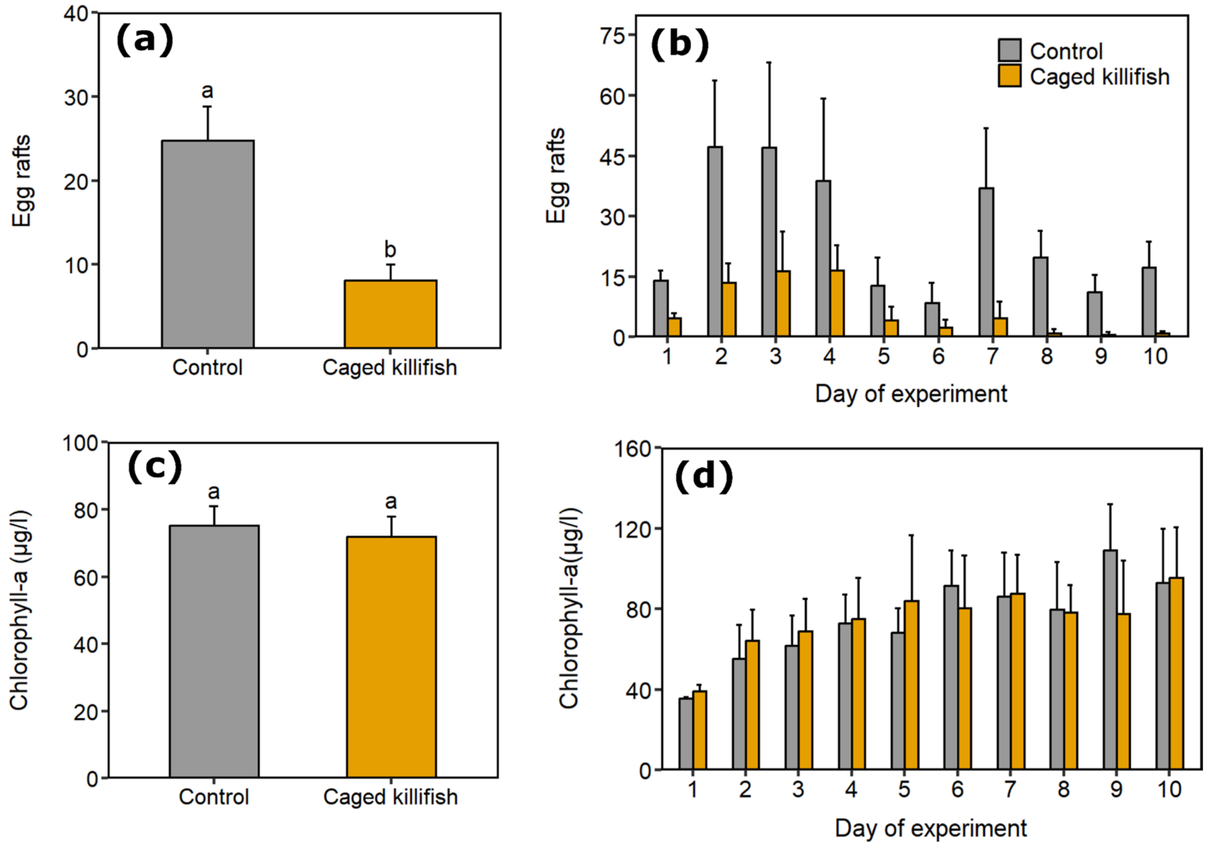

Fig. 2 Variation in the number of *Culex* egg rafts (mean ± se) deposited in the control, and caged killifish treatments over the entire duration of the experiment (**a**), and on each day of the experiment (**b**). Mean concentration of chlorophyll-a (µg/l) in the control, and caged killifish treatments over the whole duration of the experiment (**c**), and on each day of the experiment (**d**). Letters on error bars show significant differences

Table 2 Mean number (mean ± se) of deposited *Culex* egg rafts and mean concentration (mean ± se) of chlorophyll-a (µg/l) during the first and second experiments

Treatment	Caged fish		Free swimming fish	
	Egg rafts	Chlorophyll-a (µg/l)	Egg rafts	Chlorophyll-a (µg/l)
Control	24.78 ± 4.06	75.13 ± 5.98	7.28 ± 0.78	29.15 ± 3.19
Killifish	8.11 ± 1.91	71.91 ± 6.09	1.78 ± 0.27	22.82 ± 1.74

of the experiment than on other days in all treatments (all $P < 0.01$, Fig. 3d, Table S5). The predictive model showed that *Culex* oviposition was unaffected by chlorophyll-a but negatively affected by the free predator treatment where presence of a killifish in the oviposition habitat reduced oviposition ($\chi^2 = 17.17$, df = 1, $P \leq 0.001$, Table 3).

Discussion

We investigated the effect of the killifish *N. neumanni* on mosquito oviposition. We found that the presence of the Tanzanian killifish *N. neumanni* in mosquito oviposition habitat deterred *Cx. quinquefasciatus* oviposition regardless of whether the fish was swimming around in the habitat or whether the fish was caged.

Table 3 Output of predictive models (generalized linear mixed models with negative binomial error distribution) that try to explain variation in *Culex* oviposition in response to a caged killifish predator (first experiment) or a free-swimming killifish predator (second experiment). Chlorophyll-a concentration was included as a covariate

Predictor variable	Response variable: *Culex* oviposition				
	First experiment (Caged predator)			Second experiment (Free swimming predator)	
	df	χ^2	*P*	χ^2	*P*
Predator treatment	1	8.52	0.0035	17.17	<0.001
Chlorophyll-a	1	12.69	0.00037	0.39	0.53

This indicates that the most likely cues used by the mosquito for predator detection will be chemical cues.

Lower oviposition in the killifish than in the control mesocosms indicate that gravid *Cx. quinquefasciatus* mosquitoes can detect cues of this predator and thus many of them decide not to oviposit (− 71% in response to a free-swimming predator, − 68% in response to two caged predators). This experiment suggests that in the field, the killifish *N. neumanni* might also be able to reduce *Cx. quinquefasciatus* oviposition. Given that mosquitoes oviposit at night (Why et al. 2016) and ovipositing mosquitoes are unlikely to be able to visually detect predators well in an often-murky aquatic medium, particularly at night (Blaustein et al. 2003). The strong avoidance of caged fish pools by the *Culex* mosquitoes is thus

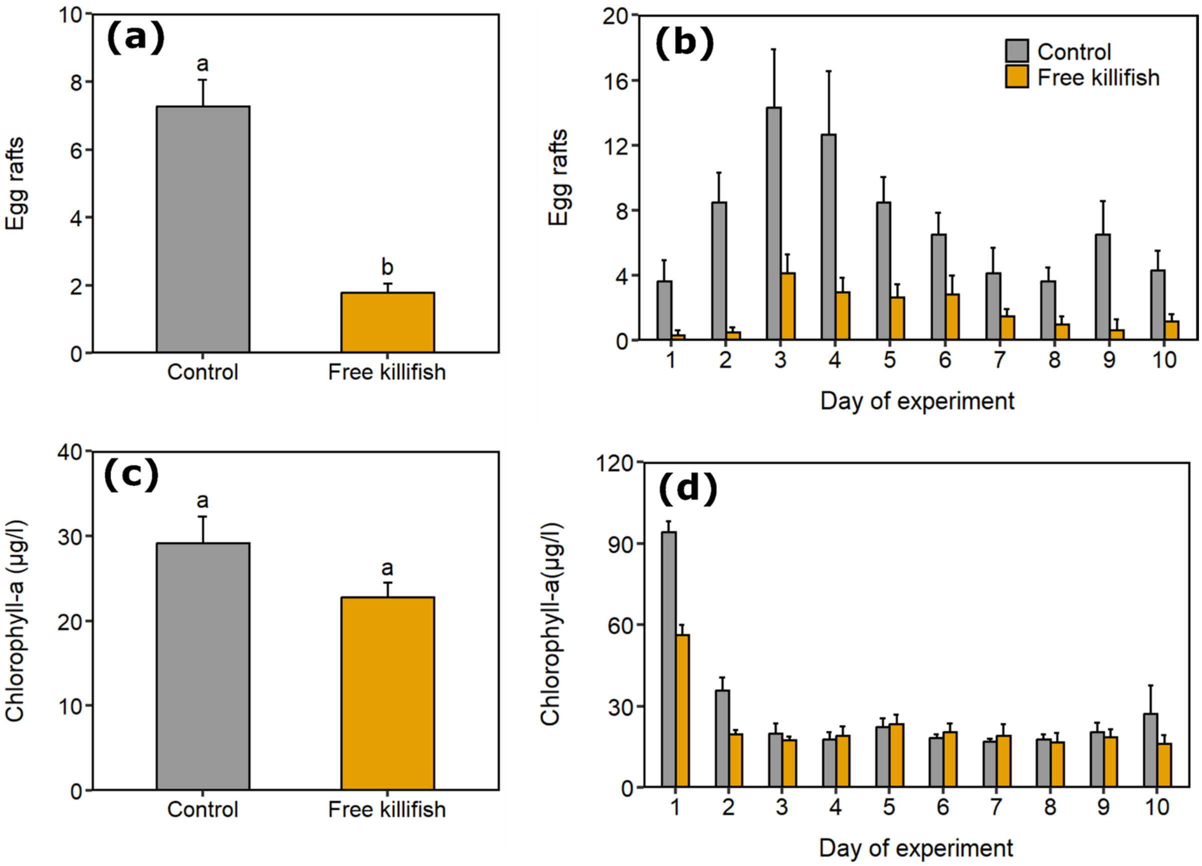

Fig. 3 Variation in the number of *Culex* egg rafts (mean ± se) deposited in the control, and free killifish treatments over the whole duration of the experiment (**a**), and on each day of the experiment (**b**). Variation in the mean concentration of chlorophyll-a (µg/l) in the control, and free killifish treatments over the whole duration of the experiment (**c**), and on each day of the experiment (**d**). Letters on error bars show significant differences

attributed to detection of fish released chemical cues by mosquitoes via chemoreceptors in their bodies, and not to other predators because these were immediately removed from mesocosms when seen. This ability is linked to natural selection which ensures that preys that co-occur with predators evolve mechanisms to recognize and avoid predation risks (Eveland et al. 2016). Mosquitoes may detect volatile chemicals from the air via olfactory mechanism or, in the case of non-volatile chemicals, by a gustatory mechanism involving direct contact with the water (Silberbush and Blaustein 2008). Oviposition habitat selection behavior is common in insects including mosquitoes, most likely because of the clear fitness benefits (Silberbush and Blaustein 2011). The response of the *Culex* mosquitoes to the free killifish is not linked to chemical cues alone but also to tactile cues which involved water vibrations that emanated from fish movement. It could be that water agitation by the moving fish prevented oviposition of some mosquitoes which managed to land on the water surface. However, this was not tested in this study, preventing separation of mosquito oviposition in response to water vibrations produced by fish movements from response due to fish kairomones. Moreover, this would still not be a reliable mode of predator detection by a mosquito because ovipositing mosquitoes in the air or on water surface are not likely to be able to distinguish well between vibrational cues caused by fish movement and the vibrations caused by numerous other non-predaceous animals in the water (Blaustein et al. 2003). In both experiments visual cues were not expected to be important for mosquitoes for predator detection. Chemical cues were the most reliable mode of predator detection in both experiments.

The few available previous studies on the potential of killifish for biocontrol of mosquitoes focused only on the consumptive effect of the fish on larval mosquito populations (Matias and Adrias 2010; Vanderplank 1941). Vanderplank (1941) confirmed for the first time the predation efficacy of killifish on mosquito larvae using *N. taeniopygus.* Based on this result, he suggested the fish might be used as an antimalarial agent in East Africa where it is indigenous. In subsequent years, Vanderplank (1941) initiated deliberate field introductions of the fish into temporary pools for mosquito control from the vicinity of Old Shinyanga to other regions in Tanzania (Dodoma area), Uganda, Kenya, and Swaziland (Reichard et al. 2010). However, this introduction largely failed to sustain viable populations because the evidence from numerous sampling efforts which have been made in many of these areas over decades since these introductions show that *N. taeniopygus* did not survive (Reichard et al. 2010). When Matias and Adrias (2010) through a mesocosm experiment confirmed the efficacy of mosquito larvae predation by *N. guentheri*, they also suggested the fish as a potential mosquito control agent which could be introduced in temporary ponds as diapausing embryos. Their suggestion was strongly criticized by Reichard et al. (2010) on the grounds that the idea was likely to be similarly unsuccessful as the Vanderplank initiative. First: successful introduction of killifish in temporary pools strongly depends on the availability of suitable soil conditions. It has been suggested that a clay-rich alluvial vertisol (Cellerino et al. 2016; Reichard et al. 2009) is necessary to preserve the diapausing eggs in the sediment during the dry seasons. While this soil is very common in East Africa, Central Africa, and Southern Africa, in all likelihood most of the mosquito habitats in the region are on different soils, limiting the introduction success of killifish, without even considering other autecological requirements. Second: studies on gut contents of field collected *Nothobranchius* suggest that mosquito larvae are a rare component of the diet of killifish which mainly feed on crustaceans (Cladocera, Copepoda, Ostracoda and Conchostraca) (Polačik and Reichard 2010). Lastly: a large number of mosquito larvae survive in the wide margins of natural pools overgrown by thick grass vegetation in water too shallow for *Nothobranchius* fishes to reach which prevents the fish from eradicating mosquito larvae in the wild. Interestingly, Reichard et al. (2010) neglected the potential of killifish to reduce larval mosquito populations through oviposition habitat selection which could be more effective than mosquito larval predation. In this study we have demonstrated that gravid mosquitoes can detect killifish via kairomones they emit, and that this mechanism alone can reduce mosquito larvae in temporary pools.

It is known that predators are not equally dangerous to a prey and different prey species are thus expected to respond differently to predators depending on the perceived risk (level of vulnerability) predators pose to a prey (Eveland et al. 2016; Roberts 2014; Silberbush and Resetarits 2017). Nonetheless, there is evidence that some mosquitoes cannot recognize kairomones from some predators despite the high predation risk. For example, using mesocosm experiments gravid *Cx. tarsalis* failed to recognize chemical cues from the fish fathead minnow *Pimephales promelas*, while the same mosquito was deterred by the fish arroyo chub *Gila orcutti* (Why et al. 2016). Also, gravid *An. gambiae* s.l did not recognize chemical cues from the fish *Epiplatys spilargyreius* which was able to deter oviposition by the gravid *Cx. quinquefasciatus* mosquito (Louca et al. 2009). All these contradicting results stress the importance of testing the efficacy of suggested predator kairomones before their adoption for mosquito control.

Abundance of planktonic algae quantified as concentration of chlorophyll-a seemed to reduce oviposition in both control and caged killifish treatments. In these treatments the concentration of chlorophyll-a increased with experimental duration and was highly correlated with the concentration of phycocyanin a proxy for cyanobacteria abundance. Cyanotoxin is known to be lethal to mosquito larvae, and because mosquitoes are equipped with the ability to assess habitat suitability for their offspring, it could be that to some extent *Culex* mosquitoes avoided ovipositing in these mesocosms. Munga et al. (2013) demonstrated that *An. gambiae* s.l laid more eggs in microcosms (diameter: 35 cm, depth: 15 cm) with fresh water (day 0) or water aged for five days than in microcosms with water aged for more than five days (i.e., 10, and 15 days). In their experiment concentration of chlorophyll-a also increased with experimental duration. Similarly, Eneh et al. 2019 showed that *Anopheles arabiensis* mosquito laid fewer eggs in mesocosms (diameter: 55 cm) with water that were aged for four and 17 days than in mesocosms with fresh water (day 0). In their experiment concentration of chlorophyll-a also increased with experimental duration. It could be possible that prior to oviposition, gravid *Cx. quinquefasciatus* can gauge and detect the level and type of planktonic algae in the habitat and opt for alternative habitat with the amount and type of algae favorable for the survival of their offspring. In general, despite its negative effect on *Cx. quinquefasciatus* oviposition, abundance of algae did not mask the effect of *N. neumanni* oviposition habitats selection by the *Cx. quinquefasciatus* mosquito.

We demonstrated that the presence and the chemical cues of the killifish *N. neumanni* which is endemic to Tanzania can strongly reduce *Cx. quinquefasciatus* oviposition. At first sight introducing fish might seem to be a cheap tool to control mosquitoes in some permanent water bodies. However, the available evidence suggests that most of these attempts have not been very successful and those happened to succeed regularly led to ecological damage to the receiving ecosystem (Azevedo-santos et al. 2017). For example, Pyke (2008) reported that introduction of *G. affinis* and its close relative *G. holbrooki* into permanent water bodies for mosquito control reduced densities of aquatic invertebrates such as rotifers, crustaceans, backswimmers, water beetles, and odonata larvae. It also led to declines and disappearance of a number of amphibian and fish species. Instead, reintroduction of indigenous fish species in their natural habitats is generally preferred over the introduction of exotic species since they have lived, adjusted, and balanced with the local aquatic fauna and flora and therefore exhibit no adverse ecological effect to native biota (WHO 2013). Our findings shade light on the potential of *Nothobranchius* killifish for use in mosquito control. Local reintroduction of this killifish into its native habitats is also not expected to pose risk to local flora and fauna. However, *Nothobranchius* killifish reintroduction is only feasible in ponds with suitable substrate (clay vertisol soil).

Many killifish species have become exceedingly rare and local reintroduction programs that bring them back to suitable temporary ponds might not just help the killifish themselves but also could make these habitats less suitable for mosquitoes. In this part of Tanzania, killifish are not likely to be important in the fight against malaria since the local *Anopheles* vector mosquitoes have a different habitat preference and can be found in very small ephemeral puddles and pools. In other parts of Africa (e.g., in Kassala town, eastern Sudan, and in Kasayani village in lower eastern Kenya) *Anopheles* does use temporary ponds (Hamza and el Rayah 2016; Mwangangi et al. 2009) but lack of suitable soil there might prevent establishment of killifish. Due to their autecological needs only a subset of ponds (with clay vertisol soil) in a region is likely to be suitable to sustain killifish populations. The use of annual killifish for mosquito control in regions where they are endemic may therefore have limited potential. During integrated mosquito control program, environmentally friendly control methods such as bio-larvicides *Bacillus thuringiensis* var *israelensis* and *Bacillus sphaericus* or insect growth regulators (IGR) such as methoprine can be applied in ponds that cannot naturally support viable populations of killifish. If isolation of killifish kairomones would be possible, the chemicals could be developed into a mosquito control strategy and used in ponds which cannot sustain killifish populations (i.e., without alluvial vertisol soil), and in other habitats such as ephemeral small pools and puddles where *Anopheles* breed. However, isolation of the exact molecules within the complex mixture of metabolites produced by fishes and associated micro-organisms has thus far been unsuccessful which prevents possible applications for chemical based larval control programs (Beklioglu et al. 2006). Disentangling chemical cues emanating from bacteria in fish mucus and the fish itself will be a substantial step towards isolation of fish kairomones.

Since mosquito oviposition response to a predator is predator specific, future studies should check whether chemical cues from *N. neumanni* that deterred oviposition by *Culex* mosquitoes may also deter other mosquitoes. This is particularly relevant for African malaria mosquitoes such as *An. gambiae* s.l for which the response to predator kairomones is still unclear. Though we successfully demonstrated that the presence and the chemical cues of the killifish can strongly reduce *Cx. quinquefasciatus* oviposition, the current study was limited by the relatively short duration (i.e., 10 days) and only one season over which the study was conducted. This prevented capture of the effects of longer-term and seasonal variation on mosquito oviposition in response to the presence of killifish. Also, the direct and indirect effect of the predator killifish on *Cx. quinquefasciatus* oviposition were tested separately. This design prevented comparison of outcome between the two experiments, and thus limited our understanding of which test produced stronger outcome. Joint test of direct and indirect effect of the killifish on *Cx. quinquefasciatus* oviposition would be a stronger test. Lastly, mesocosm tanks are not natural ponds. Trials in natural ponds would be necessary to verify whether the effects of killifish on mosquito oviposition observed in this study can translate into a natural context, as mesocosm experiments can sometimes be misleading when conclusions are extrapolated to natural systems (Collins et al. 2019). Considering these limitations would benefit future studies.

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Data availability All data generated and analyzed during this study are included in this published article. Supplementary information files are available online at https://doi.org/https://doi.org/10.6084/m9.figshare.25367539. View the supplementary information file for review purpose at https://figshare.com/s/6b0be066f13301d1768f

Declarations

Conflict of interest We are declaring that we authors do not have any competing nor conflicting interests.

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