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Short Communication

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Larvicide-mediated oviposition and ovicidal activity among treehole and container-inhabiting mosquito (Diptera: Culicidae) species

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Larval application of insecticides (larviciding) is primarily conducted using a variety of biorational compounds as an essential function within integrated mosquito management. Larvicide-treated water has been sporadically investigated for deterring oviposition, but prior efforts have been primarily focused on *Aedes aegypti* (L.) with limited representation by other peridomestic or treehole species. A series of laboratory assays were conducted using 20 lb/acre (22.4 kg/ha) treatments of *Lysinibacillus sphaericus* (VectoLex FG), spinosad (Natular G30), and methoprene (Altosid XR-G Ultra) and compared to an untreated water option. These treatments were offered as a no-choice assay for *Ae. aegypti* in the laboratory and in an additional multi-choice test for *Ae. aegypti*, *Aedes sierrensis* (Ludlow), and *Culex pipiens* L. Significantly fewer *Ae. aegypti* eggs were collected from water treated with *L. sphaericus* in both the no-choice and arena tests. Significantly fewer *Cx. pipiens* eggs were deposited in water treated with methoprene, coinciding with elevated collections in water treated with spinosad. As a first report for the species, no significant trends were observed with *Ae. sierrensis*. Hatching eggs from spinosad and methoprene-treated water yielded lower success for both *Aedes* spp. We propose that gravid mosquitoes have some sensitivity towards certain larvicides and *Aedes* spp. eggs suffer ovicidal effects in treated water sources. Push effects may confound geotagged surveillance networks, such as for treehole and backyard mosquito species in peridomestic environments. However, we report that these preferences do not significantly impact ongoing control operations.

Keywords: behavior, mosquito control, ovideterrence, urban, interference

Introduction

Larval application of insecticides (larviciding) is an essential component of integrated mosquito management (Guzzetta et al. 2017, Karunaratne and Surendran 2022). This form of abatement is widely practiced by public health stewards and employs a variety of active ingredient compounds (Karunaratne and Surendran 2022). Surveillance networks, whether manually by dipping for larvae or systematically through a gridded trapping layout, are critically important. Especially given that some programs operate in limited boundaries, such as when a jurisdictional boundary does not cover the entirety of a populated area, or when the target mosquitoes only occupy a localized niche, such as in treehole mosquito programs or residential backyard management in urban environments (Buckner et al. 2021). However, larvicides could unintentionally cause mosquitoes to disperse to new areas by making local larval sources unappealing. This ecological shift could cause disruptions in surveillance networks due to irregular mosquito movement. At present, it is unclear what the risk may be for larvicides to push targeted mosquitoes away from treated areas by deterrence from ovipositing. Some experimentation has been conducted in invasive *Aedes* spp. (Ritchie and Long 2003, Butler et al. 2006, Pérez et al. 2007, Quiroz-Martínez et al. 2012) and various ecologies of *Culex* spp. (Butler et al. 2006, Michaelakis et al. 2020). Larvicide-specific preferences can

arise (Michaelakis et al. 2020), however, it can be challenging to make direct comparisons by product and species tested.

Oviposition behavior is often inconsistent, with many variables leading up to the ultimate decision to oviposit in a given source. For example, mosquitoes can be deterred from ovipositing in a specific area because of high intraspecific or interspecific competition, whether that is detected by eggs present in the habitat (Nazni et al. 2016), or already hatched larvae in the water column (Gonzalez et al. 2016). Mosquitoes can also be attracted or deterred by microbes in fermenting water (Rejmánková et al. 2005). When those microbes signal beneficial features, such as larval food (Kramer and Mulla 1979), then their removal will correspondingly reduce attraction (Ponnusamy et al. 2008). Mosquito and vector control programs already exploit ovisite selectivity for gravid surveillance by offering microbially fermented water in traps for *Aedes* and *Culex* spp. (Allan and Kline 2004, Braks and Cardé 2007, Ritchie et al. 2014, Johnson et al. 2017). However, although this microbially fermented water is used as an attractant, if the fermentation products are toxic to larvae (Hwang et al. 1980) or even the eggs (Prajapati et al. 2005), it may predispose gravid females to avoid the contaminated water. This is consistent across several genera and species of mosquitoes (Hwang et al. 1980, Prajapati et al. 2005).

In general, compounds that discourage oviposition in otherwise suitable habitats are labeled as oviposition deterrents. These deterrents can range from natural byproducts (Kramer and Mulla 1979, Hwang et al. 1980) to synthetic products intentionally marketed for managing mosquito contact (Xue et al. 2001, 2006, Prajapati et al. 2005). However, the relationships between these deterrents are not always clear. For example, mosquitoes can be deterred by non-fatal skin repellents (Xue et al. 2001, Tawatsin et al. 2006), even when a hole is available in a treated membrane, allowing access to an oviposition cup (Xue et al. 2001). Conversely, it has also been observed that intoxicated mosquitoes, whether by repellents or insecticides, will still try to oviposit (Choi et al. 2016). This latter finding questions whether larvicides used in operational abatement programs might also contribute to greater mosquito dispersal, thus decreasing the utility and accuracy of surveillance efforts.

Deterrents do not have to be applied to a superficial barrier, and it has been experimentally observed that ingredients suspended in the water column at an oviposition site will still deter mosquito engagement (Hwang et al. 1980, Tawatsin et al. 2006, Xue et al. 2006). These behaviors can be measured clearly in gravid females of *Aedes, Culex,* and *Anopheles* species. For example, *Aedes* spp., will bias the total number of eggs deposited into microbially enriched ovisites and away from undesirable tap water ovisites (Wasson-Reinbold and Reiskind 2021). Similarly, in *Culex* and *Anopheles* spp., they will withhold eggs from undesirable sites when an oviposition deterrent is detected, despite stronger biological limitations for retaining eggs while gravid (Hwang et al. 1980, Prajapati et al. 2005). Given that mosquitoes can display avoidance behaviors through egg deposition, it is possible to test assumptions about larvicides, which also span a range of materials, like juvenile hormone mimics (eg methoprene), and antagonistic microbes that can kill through ingestion (eg *Bacillus thuringiensis* var. *israelensis*, *Lysinibacillus sphaericus*) or contact (eg spinosad). In our study, we treated water directly with 3 different commercial larvicides and monitored their effect in bioassays by observing how eggs were distributed across sources using a no-choice assay for *Aedes aegypti* (L.) and in an additional multi-choice test with the yellow fever mosquito, *Ae. aegypti,* the Western treehole mosquito, *Aedes sierrensis* (Ludlow), and the northern house mosquito, *Culex pipiens* L. It is widely accepted to re-sample treated sites to ensure the continuing efficacy of a product. But by examining how eggs are distributed among treated water, we can infer if mosquitoes may subsequently alter where they oviposit after systematic treatment with mosquito larvicides.

Materials and Methods

Mosquitoes selected for testing included the 1952 Orlando, Florida strain of *Ae. aegypti*, a 2016 Salt Lake City, Utah strain of *Cx. pipiens*, and a 2018 Sonoma County, California strain of *Ae. sierrensis*. All species were reared in laboratory colonies grown and maintained at the Salt Lake City Mosquito Abatement District. Mosquito larvae were hatched in nutrient broth and adults were housed in flight cages stocked with a 10% sucrose solution. All rearing and experimentation were conducted in consistent environmental conditions of 27 ± 1 °C temperature and 70 ± 5% relative humidity. Lighting conditions were held at 12:12 light:dark with an incremental dawn/dusk cycle as the light phase shifted. Three days prior to assay, adults aged 7 to 10 d were blood fed using a custom membrane feeding apparatus (Dewsnup et al. 2023) loaded with citrated bovine blood (Lampire Biological Labs, Inc., Pipersville, PA). After allowing 48 h for egg development and females to become gravid, mosquitoes were transferred to bioassay cages for oviposition study.

All assays were carried out in mesh-sided, rectangular flight cages measuring 40.64 cm × 30.48 cm × 40.46 cm (Restcloud Butterfly Habitat: B08BXMJ92Q, Sihai Muze Technology, Ltd., Chengdu, CHN) stocked with 50 gravid mosquitoes. Oviposition cups were created from 473 ml clear drinking cups (polyethelene, ASF Tashi LLC, Pittsfield, MA) and were lined with seed germination paper (#6512981311, Anchor Paper Co., Saint Paul, MN). Strips were cut to 13 cm × 19 cm and inserted as a roll into the cups such that 1 to 2 cm of seed germination paper was apparent above the rim of the cup. A supply of 10% sucrose solution was provided in a small vial with a white, paper towel wick for the duration of the experiment. Paper-lined cups were filled with untreated reverse osmosis water, or maximum label rates at 20 lb/acre (22.4 kg/ha) of either VectoLex FG (7.5% *Lysinibacillus sphaericus* 2362, Serotype H5a5b, Strain ABTS 1743, Valent BioSciences Corporation, Libertyville, IL), Natular G30 (2.5% spinosad, Clarke Mosquito Control Products, Inc., Roselle, IL), or Altosid XRG Ultra (1.6% (S)-Methoprene, Central Garden & Pet Company, Schaumberg, IL). These treatments were conducted with 0.693 g of product in 227 g (= 227 ml) of water. Assuming a 6-inch depth on the acre for the max label rates, the estimated saturation in water for these bioassays would be 0.75 ppm, 0.25 ppm, and 0.16 ppm of the *Lsph*, spinosad, and methoprene, respectively.

Assay development for no-choice trials was carried out for *Ae. aegypti* using only one treatment option at a time and replicated 4 times for each of the 4 treatment groups (water, *Lsph*, spinosad, methoprene). This was to verify that maximum label rates could still be informative to oviposition, as the test concentrations of active ingredient resulting from these products were lower than in prior experiments (Ritchie and Long 2003, Pérez et al. 2007, Quiroz-Martínez et al. 2012). No choice assays were analyzed as the mean eggs collected divided by the female count, then using an ANOVA with a Tukey post-hoc test with larvicide-treated water groups as factors. After verifying oviposition behaviors in the no-choice trials, larger four-choice tests were conducted using all 4 treatment groups simultaneously. These choice arenas were replicated 9 times per treatment for each of *Ae. aegypti*, *Ae. sierrensis,* and *Cx. pipiens*. Multi-treatment arena trials were taken as a proportion of the count (numerator) of total eggs across the cage regardless of treatment (denominator) and then analyzed using a 2-way ANOVA with interaction. The placement of treated/untreated cups was randomized in each

replicate to mitigate light-orientation biases that may occur. In both trial types, mosquitoes were allowed 7 d to oviposit before substrates were removed and eggs, whether from rafts or individuals on seed germination paper, were counted under a light dissection scope. Eggs were then withheld in rearing conditions to observe hatching in the original treated water. For egg rafted, they were allowed to rest as normal until hatching. For those on seed germination papers, the eggs were loosened from their containers and reoriented to totally submerge the eggs below the water line. Hatching success was averaged on percentages nested from the collected egg totals by treatment. These nested average percentages across species by treatment type were also analyzed with a 2-way ANOVA with interaction. All statistical analyses were conducted using R v. 4.2.0 (v.4.2.1, The R Foundation for Statistical Computing, Vienna, Austria) via RStudio (v. 3.3.0, RStudio PBC, Boston, MA).

Results

Numbers of eggs from *Ae. aegypti* across water, spinosad, and methoprene were similar and not significantly different (Fig. 1A). However, there were significantly fewer eggs collected in *Lsph* treated ovicups than spinosad or methoprene ($F_{3,16} = 0.642$, $P = 0.048$). No eggs were observed to be oviposited on the sugar water wick during any of the experiments. Eggs being laid at all affirmed that despite larvicide-treated water, gravid mosquitoes would still oviposit even in water they did not prefer (ex: *Lsph*). In the multi-choice arena assays, the interaction between species tested and the treatments used was significant ($F_{6,108} = 4.792$, $P = 0.0002$), but the between-species effects alone were not. Rather, the treatments drove all the variation in results ($F_{3,108} = 5.448$, $P = 0.002$) with both *Ae. aegypti* and *Cx. pipiens* having significantly skewed egg deposition toward plain water and water treated with spinosad, respectively (Fig. 1B). For *Ae. aegypti,* the lowest proportion of eggs were recovered from water treated with *Lsph*. For *Cx. pipiens*, the lowest proportions were collected from water treated with methoprene. There were no significant differences across treatments for where *Ae. sierrensis* deposited eggs (Fig. 1B). Hatching of eggs harvested from arenas was significantly lower for *Ae. aegypti* and to a greater extent with *Ae. sierrensis* as a result of both spinosad and methoprene treatments (Fig.2; $F_{3,101} = 72.726$, $P < 0.0001$). The interaction between species and treatment was significant ($F_{6,101} = 11.702$, $P < 0.0001$), and the hatch success of *Cx. pipiens* was generally unaffected by treatment exposures.

Discussion

Larvicides can discourage mosquito oviposition and push egg deposition away from water treated with certain products. Avoidance behaviors can be complex because even crowding density (Gonzalez et al. 2016, Nazni et al. 2016), fermentation cues (Kramer and Mulla 1979, Ponnusamy et al. 2008), and risk of fatality (Hwang et al. 1980, Prajapati et al. 2005) can change oviposition preference in the field. We observed this complexity in data collection when *Ae. aegypti*, a species previously shown to be refractory to several types of larvicides in water (Ritchie and Long 2003, Pérez et al. 2007, Quiroz-Martínez et al. 2012), had deposited fewer eggs in water treated with a bacterial larvicide (*Lsph*). In contrast, *Cx. pipiens* deviated from some prior findings by depositing fewer eggs in water treated with an insect growth regulator (methoprene) (Butler et al. 2006). Furthermore, *Cx. pipiens* avoided ovipositing in water treated with a microbial byproduct (spinosyns), contradicting some prior results with *Cx. pipiens* biotype *molestus* (Michaelakis et al. 2020).

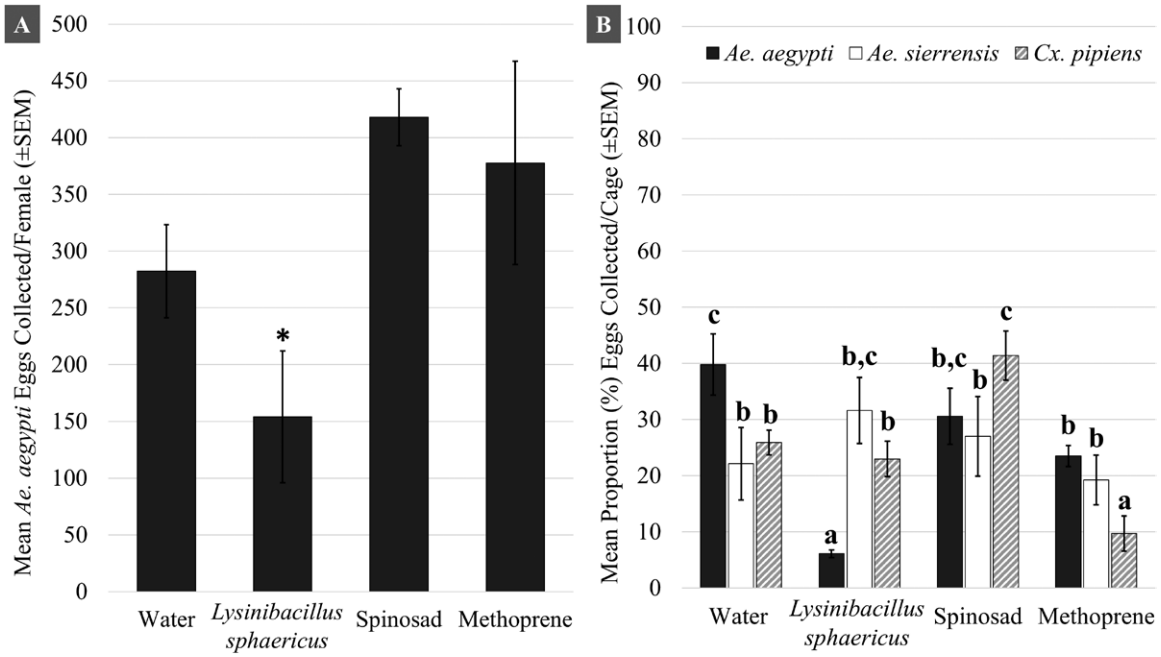

Fig. 1. Oviposition cups contained reverse osmosis water (control) or 20 lb/acre (22.4 kg/ha) treatment rates of either *Lysinibacillus sphaericus* (VectoLex WDG), spinosad (Natular G30), or methoprene (Altosid XR-G Ultra). (A) No-choice oviposition assays with *Aedes aegypti* (L.), whereby a single cup was admitted for egg collections, were analyzed by the mean number of eggs collected per female mosquito (50 per cage). Asterisk denotes significantly fewer eggs ($F_{3,16} = 0.642$, $P = 0.048$). (B) Choice arena oviposition assays were conducted with *Aedes aegypti, Ae. sierrensis*, or *Culex pipiens*, whereby 4 treatments in separate cups were admitted for egg collections. Data were interpreted on the proportion of eggs, derived from the count in a selected treatment (numerator) relative to the total eggs collected across all treatments in the respective cage of assay (denominator) ($F_{3,108} = 5.448$, $P = 0.002$). Graph is shown with standard error of the mean as I-bars and annotated significance from lowest (a) to highest (c) egg collection groupings.

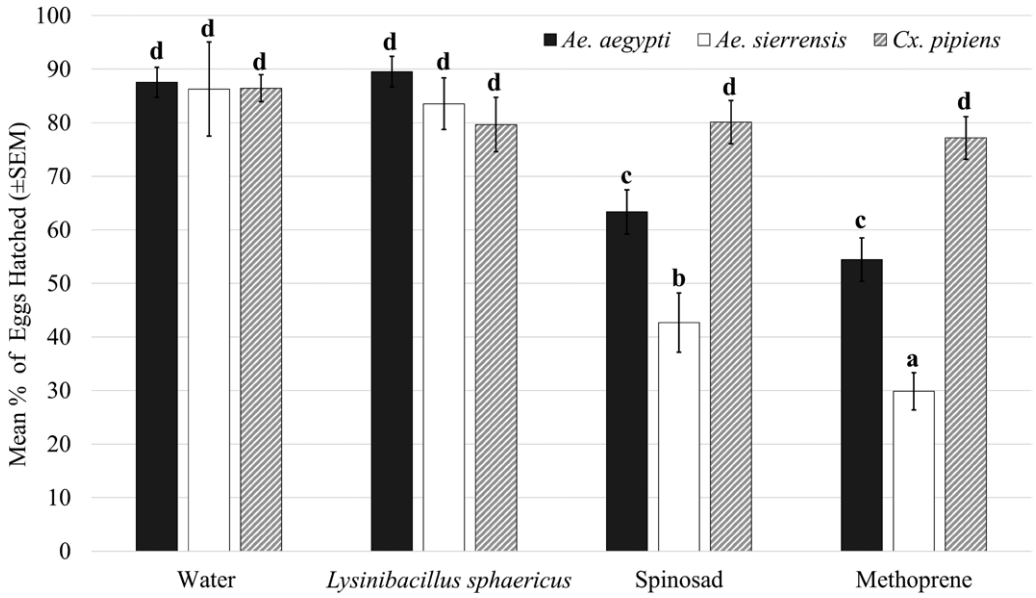

Fig. 2. Eggs from *Aedes aegypti* (L.), *Ae. sierrensis* (Ludlow), or *Culex pipiens* L. were collected and hatched from oviposition cups containing reverse osmosis water (control) or 20 lb/acre treatment rates of either *Lysinivacillus sphaericus* (VectoLex WDG), spinosad (Natular G30), or methoprene (Altosid XR-G Ultra). Graph is shown with standard error of the mean as I-bars and annotated significance from lowest (a) to highest (d) egg collection groupings ($F_{3,101} = 72.726$, $P < 0.0001$).

Whereas the observations that neither methoprene nor spinosad deterred oviposition by *Ae. aegypti* is generally in agreement with prior studies (Ritchie and Long 2003, Quiroz-Martínez et al. 2012).

If larvicides successfully deter oviposition, retained eggs may not necessarily be healthy enough to hatch later (Xue et al. 2004). And perhaps more importantly, eggs that must be submerged, such as those laid by *Aedes* spp., can be interrupted from hatch with ovicidal activity from methoprene or spinosyns. Interestingly, the eggs from *Cx. pipiens* did not experience any differences in hatch success, perhaps because of the limited surface area of a raft floating on top of the treated water. This may or may not apply to floating individual eggs, such as by *Anopheles*, which may have more turbulent contact with water (Ebrahimi et al. 2014). The ovipositional deterrence and ovicidal activity against mosquitoes may affect mosquito control programs that rely on geotagged networks to monitor mosquito populations, since shifts in oviposition could push the distribution of mosquito species into poorly monitored areas or outside jurisdictional boundaries. However, repeated exposure to given larvicides will reduce avoidance over generations, suggesting a potential adaptation to deterrents over time (Kaur et al. 2003).

Of course, a natural caveat is that our data was derived from laboratory studies where temperature, humidity, and light were constant and there is no meaningful, predation, competition, microhabitat variation, climatological, and environmental impact. However, this is a new report for *Ae. sierrensis* and a collection of screening results across multiple peri-domestic vectors and multiple larvicide classes in one place. This study pertains more to fatal stressors in water (Hwang et al. 1980, Prajapati et al. 2005), which have received less attention than adult-oriented control (Choi et al. 2016). In addition, our investigations add new information on ovicidal options, which have been documented in skin repellents (Prajapati et al. 2005), but not often with water-formulated larvicide products (Pérez et al. 2007). Despite finding evidence that larvicides can influence oviposition decisions, we do not believe that surveillance within operational mosquito control programs is in any way jeopardized by our findings. The inconsistent nature of larvicide avoidance (Ritchie and Long 2003, Butler et al. 2006, Pérez et al. 2007, Quiroz-Martínez et al. 2012, Michaelakis et al. 2020), and the tendency of mosquitoes to become refractory to insecticide cues (Kaur et al. 2003), reduce the immediate risk of oviposition deterrence in the broader operational context. In contrast, the added utility of reducing successful hatch in eggs submerged in larvicide-treated water may be actually desirable, and may confer annual benefits by reducing sequestered egg caches in treated areas. Future research into secondary or sub-lethal effects of larvicides and adulticides could identify other benefits that reduce contact with mosquitoes and the pathogens they transmit.

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Author contributions

Kai Casci (Data curation [equal], Investigation [lead], Methodology [equal], Writing—original draft [lead], Writing—review & editing [supporting]), Andrew Dewsnup (Conceptualization [lead], Methodology [supporting]), Ary Faraji (Project administration [supporting], Resources [lead], Supervision [equal], Writing—review & editing [equal]), and Christopher Bibbs (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Investigation [supporting], Methodology [supporting], Project administration [equal], Supervision [lead], Validation [lead], Visualization [lead], Writing—original draft [equal], Writing—review & editing [equal])

Conflicts of interest. None declared.

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