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Duckweeds produce strong oviposition avoidance and high larval mortality in invasive *Aedes* mosquitoes

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Abstract

Background We examined how two invasive mosquito species, Asian tiger mosquitoes, *Aedes albopictus*, and Asian rock pool mosquitoes, *A. japonicus*, responded to the presence of duckweeds when ovipositing and how these plants affected *Aedes* larval survivorship found. Since duckweeds have been shown to increase egg-laying but kill mosquito larvae in some species, they could be used as a natural form of biocontrol. A total of four experiments were conducted in 2019 and 2022 that quantified the number of *Aedes* eggs laid and the percent survival of their larvae in sites with and without the duckweeds *Spirodela polyrhiza* and *Wolffia arrhizal*.

Results Females of both species laid significantly fewer eggs in sites with duckweeds, and these plants significantly increased larval mortality. In *A. japonicus*, larval survivorship was 0% with duckweeds.

Conclusions Unfortunately, our results suggest that biological control of *Aedes* mosquitoes using duckweeds appears less promising given the ability of females to detect and avoid these plants.

Keywords Invasive species, Mosquitoes, Oviposition, Ecological trap, Duckweeds, *Aedes*, Biological control

Background

Invasive species represent a major threat to global biodiversity (Simberloff et al., 2013) and can have negative economic impacts within their invaded range (Diagne et al., 2021). This is well exemplified by the recent and rapid spread of mosquitoes in the genus *Aedes* (*Aedes aegypti*, *A. albopictus*, *A. japonicus*) given their ability to transmit multiple viral human pathogens (Juliano & Lounibos, 2005), and negatively affect native species abundances (Juliano & Lounibos 2005). The extensive use of artificial water sources, such as gutters, tires and trash, as preferred oviposition sites by *Aedes* mosquitoes (Crans, 2004; Juliano & Lounibos, 2005) exacerbates the harmful interactions between humans and invasive *Aedes*

species, as mosquito abundance often increases with human population density in urban and suburban areas (Kollmenakis et al., 2021).

An extensive body of research exists examining factors affecting mosquito oviposition preference and larval mortality (Bently & Day, 1989, Vonesh & Blaustein, 2010, Day, 2016, Mwingira et al., 2020). Habitat selection theory predicts that adult female mosquitoes choose oviposition sites with a high likelihood of egg and larval survivorship (oviposition preference predicts larval performance, Blaustein, 1999). However, females can be induced to lay eggs in sites with high larval mortality producing an ecological sink or trap (Pulliam & Danielson, 1991, Bellile & Vonesh, 2016, Binckley & Thomas, 2017, Albeny-Simões et al., 2014). For example, some, but not all, *Culex pipiens* populations oviposit significantly more egg rafts at sites containing the duckweed (*Lemna minor*) resulting in high larval mortality (Baz, 2017, Cuthbert et al., 2020a).

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Duckweeds are common free-floating aquatic plants grouped into four genera within the family Lemnaceae that form dense surface mats in ponds and wetlands (Hillman, 1961). Scientists have long recognized the inverse relationship between duckweed presence and the absence of mosquito larvae (Matheson, 1930). Using duckweeds to influence both oviposition and larval mortality is a promising method to control disease-carrying mosquitoes (Cuthbert et al. 2020a). However, this work has focused primarily on *Culex* species (Eid et al., 1992a, 1992b; Baz, 2017, Cuthbert et al., 2020a, 2020b) and how egg-laying *Aedes* females and their resulting larvae are affected by duckweeds is largely unknown (Judd & Borden, 1980). Thus, we examined how two invasive *Aedes* species (the Asian tiger mosquito, *A. albopictus*, and the Asian rock pool mosquito, *A. japonicus*) responded to the presence of duckweeds when ovipositing and how these plants affected larval survivorship.

Methods

Our study site is a forested area at Arcadia University (Montgomery County, PA, USA) $\approx$ 65 years post-succession and dominated by tulip (*Liriodendron tulipifera*) and sugar maple (*Acer saccharum*) trees. Here, *A. japonicus* breeds first, from mid-May to early August while *A. albopictus* are generally found from early July, dominate by late August and continue to deposit eggs until late October (Binckley, 2017; Binckley & Thomas, 2017). There is much annual variation to this phenology, producing either short or extensive temporal overlap when both species oviposit at the same time. Due to these differences, only *A. japonicus* oviposition occurred during experiment 1, while both *A. japonicus* and *A. albopictus* oviposition occurred in experiment 3 (see below).

Experiment 1: *Aedes japonicus* oviposition

We established 12 mosquito oviposition sites from July 1, 2019, to July 10, 2019. Each site consisted of a 100-L black plastic tub 0.6 m in diameter and 0.3 m tall, filled with 75 L of creek water. Sites were arranged into six spatial blocks of two tubs each with one treatment (control or 36.0 g of the duckweeds *Spirodela polyrrhiza* and *Wolffia arrhiza*) randomly assigned to tubs within blocks using a random number generator (Fig. 1), resulting in a total of six controls and six duckweed oviposition sites. Blocks were $\approx$ 30 m apart and tubs within blocks were 1 m apart.

We collected duckweeds on June 25, 2019, from a fishless pond at the Schuylkill Center for Environmental Education located in Philadelphia, PA, USA. The two duckweed species (*S. polyrrhiza* and *W. arrhiza*) were not separated prior to their addition to sites on July 1, 2019; thus, the proportion of each species was unknown. Since *Aedes* eggs are laid right above the



Fig. 1 View of one block of treatments used in experiment 1. Duckweed fully covered the water surface of tubs and are hypothesized to produce visual/chemical cues affecting *Aedes* oviposition and chemical/mechanical factors that induce high larval mortality

waterline, we also inserted 4 tongue depressors (hereafter ovisticks), each wrapped in a brown paper towel and secured with tape, into each site to allow for egg deposition (Binckley & Thomas, 2017; see Fig. 1). Furthermore, we added a single HoboTemp data logger to all 12 oviposition sites that measured water temperature (C) each hour for the duration of the experiment to test if duckweeds reduced water temperature given their propensity to completely cover water surfaces (Fig. 1).

We checked oviposition sites daily for integrity and collected/replaced ovisticks on July 5 and did a final ovistick collection on July 9, 2019. Ovisticks were returned to the laboratory to count eggs under a dissecting microscope. We air-dried ovisticks for two days before placing them in tubs filled with stream water (four tubs per treatment, 45 cm length $\times$ 25 cm width $\times$ 20 cm depth, water depth 5 cm) to allow egg hatching and larval identification using Farajollahi and Price (2013). All dataloggers were removed on July 10, 2019.

Experiment 2: *Aedes japonicus* larval survivorship

We conducted a laboratory experiment examining how duckweeds affected *A. japonicus* larval survivorship by establishing 12 larval survivorship cups (six controls and six with 3.5 g of duckweed) each consisting of a 475-ml black plastic cup filled with creek water (Binckley, 2017; Binckley & Thomas, 2017). Treatments were randomly assigned to cups within the six blocks, and 10 *A. japonicus* larvae from an earlier experiment were randomly assigned to cups on July 16, 2019. Larvae were collected from multiple hatching tubs into groups of 10, and these were randomly assigned to blocks then cup within blocks. Surviving larvae, those still moving and not discolored or decayed, were counted on July 26, 2019.

Experiment 3: *Aedes albopictus* and *Aedes japonicus* oviposition

We established 30 mosquito oviposition sites (15 controls and 15 with duckweed) in a forested area at Arcadia University from June 14 to July 5, 2022. Each site consisted of a 475-ml black plastic cup with four small holes drilled near the top to prevent overflow with rain. Smaller cups were used for ease of setting up experimental units and for higher replication. Each cup was placed in a shallow (≈ 5 cm) hole to prevent tipping, and we inserted two ovisticks into each cups to allow egg deposition (see Binckley, 2017; Binckley & Thomas, 2017). Cups were arranged into 15 spatial blocks of two cups each with one treatment (control or 3.5 g of the duckweeds *Spirodela polyrhiza* and *Wolffia arrhiza*) randomly assigned to cups within blocks. Blocks were ≈ 25 m apart and cups within blocks were 1 m apart.

On June 21 and June 28, we collected/replaced ovisticks, with a final collection on July 5, 2022. As in experiment 1, we counted eggs under a light microscope, dried them for two days before placing them in tubs to allow for egg hatching and larval identification. A mixture of *A. japonicus* and *A. albopictus* was identified (Farajollahi & Price, 2013), and we used *A. albopictus* for a larval survivorship experiment.

Experiment 4: *Aedes albopictus* larval survivorship

We conducted a laboratory experiment examining how duckweeds affected *A. albopictus* larval survivorship by establishing 10 larval survivorship cups (five controls and five duckweed) as in experiment 2 (see also Binckley, 2017; Binckley & Thomas, 2017). Control and duckweed treatments were randomly assigned to cups within the five blocks, and 12 *A. albopictus* larvae were randomly assigned to cups on July 12, 2021. Larvae were collected from multiple hatching tubs and placed into groups of 12, and these were randomly assigned to blocks then cup within blocks. Surviving larvae, those still moving and not discolored or decayed, were counted on July 22, 2021.

Statistical analysis

All experiments utilized a randomized block design, and we analyzed the effects of block and treatment using a GLMM ANOVA. The response variable in Experiment 1 was the number of *A. japonicus* eggs laid. Similarly, the response variable for Experiment 3 were the number of *Aedes* (combined *A. japonicus* and *A. albopictus*) eggs collected. The proportion of larvae surviving was the response variable for each larval survivorship experiment. Egg count data were square root transformed, while larval survivorship data were arcsine transformed to meet ANOVA assumptions of normality

(Shapiro–Wilk test) and homogeneity of variance (Levens’s test). Since normality and homogeneity of variance assumptions were violated for both larval survivorship experiments, a Mann–Whitney *U* test was used to analyze these data. Data analysis was conducted using SAS for Windows version 9.3 with $\alpha = 0.05$.

Results

Experiments 1 and 2 *Aedes japonicus* oviposition and larval survivorship

A total of 9,883 *A. japonicus* eggs were collected in experiment 1 with 93.5% being laid in controls as females strongly avoided sites containing duckweeds ($F_{1,5} = 69.22$, $p < 0.0001$, Fig. 2), whose presence resulted in 100% larval mortality ($U = 36.0$, $p < 0.0013$, Fig. 2). Water temperature with duckweeds (average $23.21\text{ }^{\circ}\text{C} \pm 0.06$ SE) did not differ significantly from controls (average $23.44\text{ }^{\circ}\text{C} \pm 0.11$ SE, $F_{1,5} = 0.14$, $p = 0.07$). No hatched eggs, as indicated by a ruptured chorion (Mundim-Pombo et al., 2021), were observed on ovisticks.

Experiments 3 and 4 *Aedes albopictus/japonicus* oviposition and *A. albopictus* larval survivorship

A total of 13,035 *Aedes* eggs were collected during experiment 3, with 78.9% deposited in control, as females of both species showed a strong avoidance of duckweeds ($F_{1,29} = 62.07$, $p < 0.0001$, Fig. 3). No hatched eggs (Mundim-Pombo et al., 2021) were observed on ovisticks. A total of 3622 larvae were identified, and 43% were *A. albopictus*. Duckweed presence resulted in significantly higher *A. albopictus* larval mortality ($U = 0.0$, $p = 0.01$, Fig. 3).

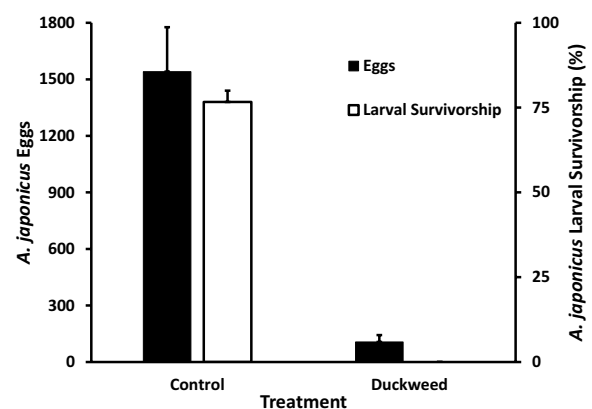


Fig. 2 Mean (± 1 SE) number of *A. japonicus* eggs (black) and % of larvae surviving (white) for treatments lacking (controls) or containing duckweeds. Females laid significantly more eggs in controls where larval survivorship was significantly higher. *A. japonicus* larval survivorship was 0% with duckweeds

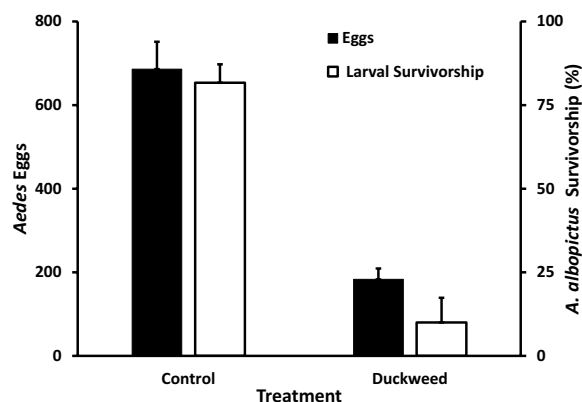


Fig. 3 Mean (± 1 SE) number of *Aedes albopictus* and *japonicus* eggs (black) and % of *A. albopictus* larvae surviving (white) for treatments lacking (controls) or containing duckweeds. Females laid significantly more eggs in controls where larval survivorship was significantly higher

Discussion

Oviposition habitat selection allows female mosquitoes to choose the environment experienced by their offspring, and natural selection favors females that detect and avoid factors producing larval mortality (Binckley & Resetarits, 2002). For example, female *Aedes* mosquitoes avoid ovipositing in sites containing duckweeds (Figs. 2, 3) that significantly increased larval mortality (Figs. 2, 3). Our results follow the preference performance hypothesis (Binckley & Resetarits, 2003) and expands upon past research examining the potential of duckweed species as natural mosquito biocontrol. However, this work has primarily focused on how these plants affect *Culex* mosquitoes.

Ovipositing *Culex* females have been documented to avoid (Eid et al., 1992a, 1992b, Yang et al., 2007), not respond (Judd & Borden, 1980) and even select (Baz, 2017, Cuthbert et al., 2019, 2020) sites containing duckweed or their chemical extracts. However, all studies are similar by repeatedly demonstrating greatly increased larval mortality (Baz, 2017; Eid et al., 1992a, 1992b) and often complete larval death (Cuthbert et al., 2020a, 2020b), with duckweeds. Minimal research on how *Aedes* responds to duckweeds mirrors our results in that ovipositing *Aedes aegypti* were shown to avoid *Lemna minor* extracts (Judd & Borden, 1980). Our experiments examining *Aedes* larval survivorship are the first that we know of, and results match those seen in *Culex*, as duckweed species clearly kill mosquito larvae across multiple genera. Examining intra- and interspecific oviposition responses within *Aedes* to duckweed species is warranted given the variation documented for *Culex*. Nonetheless, we hypothesize a generalized oviposition avoidance by

Aedes given what is known about how females select oviposition sites.

How invasive *Aedes* choose egg-laying sites is important for both population monitoring and control and multiple cues might allow females to avoid duckweeds (Figs. 2, 3). *Aedes* females clearly prefer black oviposition sites (reviewed in Marin et al., 2020) and avoid green when laying eggs (Frank, 1985; Marin et al., 2020; Yap, 1975). Duckweeds generate a thin green surface layer that might be visually detected by diurnal egg-laying species (Westby & Juliano, 2015) such as *A. albopictus* and *A. japonicus*. A simple behavioral rule of avoiding green when ovipositing could, by itself, explain our results and suggests a generalized avoidance of duckweeds by *Aedes*. If this mechanical barrier also affects adult females while ovipositing is unknown. Additionally, duckweed chemical extracts are detected and avoided by both ovipositing *Culex pipiens* (Eid et al., 1992a, 1992b) and *A. aegypti* (Judd & Borden, 1980). Duckweeds could affect aquatic microbial communities whose chemical cues influence *Aedes* oviposition (Trexler et al. 2003; Ponnusamy et al., 2008; Albeny-Simões et al., 2014) as they are highly effective at removing nitrogen and phosphorus from water. Regardless of the cue(s) used to detect and avoid duckweeds, this behavior reduces larval mortality (Figs. 2, 3) resulting from both plant chemicals and a mechanical barrier that prevents larvae respiration (Eid et al., 1992a, 1992b; Baz, 2017 Cuthbert et al. 2019, 2020). Identifying the exact mechanism female mosquitoes use to detect and respond to duckweeds could produce innovative strategies for reducing disease transmission.

Research identifying specific factors affecting mosquito oviposition habitat selection has a long history (Bentley & Day, 1989; Day, 2016; Vonesh & Blaustein, 2010), and some recent work has focused on potentially generating ecological traps or sinks to facilitate biological control. Here, characteristics of the oviposition site greatly increase both egg deposition and larval mortality (Albeny-Simões et al., 2014, Bellie & Vonesh, 2016, Binckley & Thomas, 2017, Cuthbert et al., 2020b). For example, Binckley and Thomas (2017) showed that *Culex restuans* laid significantly more egg rafts with biopesticides (*Bacillus thuringiensis israelensis* and *Bacillus sphaericus*) which resulted in complete larval mortality. Furthermore, Cuthbert et al. (2020a) demonstrated that both duckweed (*Lemna minor*) and pond dye increased *Culex pipiens* oviposition followed by duckweed induced larval mortality. How female mosquitoes respond to larval mortality itself when laying eggs is largely unknown, but could greatly reduce, or enhance, any ecological trap if females avoid or select (Albeny-Simões et al., 2014) cues from dead larvae (Binckley & Thomas, 2017. Unfortunately, our results suggest that biological control of

Aedes mosquitoes using duckweeds appears less promising given the ability of females to detect and avoid these plants.

Conclusions

Some disease-carrying *Culex* mosquitoes choose sites with duckweed plants when laying eggs, resulting in high larval mortality. The generality of this ecological trap is untested but could be highly useful as a natural biocontrol. We examined how two invasive mosquitoes, *Aedes albopictus* and *A. japonicus*, responded to duckweeds when laying eggs and how these plants influenced larval survivorship. Both *Aedes* species significantly avoided duckweed sites when ovipositing and larval survivorship was further significantly reduced. Ovipositing *Aedes* species might generally avoid duckweeds given their ability to shun the color green when laying eggs. Biological control of these invasive species using duckweeds appears less promising compared to other mosquitoes.

Abbreviation

ANOVA Analysis of variance

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Author contributions

CB conceived and designed the study. AG and KL performed the experiments. All authors analyzed the interpreted the data. CB performed the original draft preparation. All authors reviewed, edited and approved the manuscript.

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Availability of data and materials

Datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request. All data generated or analyzed during this study are included in this published article.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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