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Influence of the presence of invasive mosquitofish and submerged vegetation on oviposition site selection by gray treefrogs (*Hyla versicolor*)

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Amphibians often select oviposition sites based on a variety of cues that indicate the level of risk in the oviposition habitat. Surprisingly, the role of aquatic vegetation or habitat structure/complexity in anuran oviposition site selection has not been extensively studied even though it might affect perceived risk. We examined the effects of free-ranging invasive western mosquitofish (*Gambusia affinis*) and artificial vegetation/habitat structure on colonisation of experimental pools by gray treefrogs (*Hyla versicolor*). *Hyla versicolor* avoided ovipositing in mesocosms with *G. affinis*. The presence of artificial vegetation/habitat structure had no effect on oviposition site selection by *H. versicolor*, whether alone or in interaction with *G. affinis*. Our experiment provides evidence for the avoidance of fish, and more specifically *G. affinis*, by ovipositing *H. versicolor*; but provides no evidence for a role of vegetation/habitat structure.

Keywords: Eggs, *Gambusia affinis*, habitat complexity, *Hyla versicolor*, oviposition, vegetation

INTRODUCTION

Adults of amphibians that breed in aquatic habitats often select oviposition sites based on a variety of cues indicating the level of risk to their offspring, including predation (Pintar & Resetarits, 2017b; Resetarits et al., 2018; Smith & Harmon, 2019), desiccation or water holding potential (Rudolf & Rödel, 2005; Pintar & Resetarits, 2017b), competition (Schulte et al., 2011; Stein & Blaustein, 2015; Smith & Harmon, 2019), conspecifics (Rudolf & Rödel, 2005), and parasitism (Kiesecker & Skelly, 2000) (see also review in Blaustein, 1999; Buxton & Sperry, 2017). For most of these cues, the parent selects an oviposition site that maximises the benefit to their offspring (Pintar & Resetarits, 2017a; Hawley Matlaga, 2018), but not always perhaps due to shifts in the offspring environment indicated by the cue (e.g., historically, low levels of tannins indicated a temporary pond without fish but more recently high tannin levels in pond due to invasive plants are harmful to offspring; Dodd & Buchholz, 2018).

Surprisingly, the effect of habitat structure and complexity, including the presence of submerged and surrounding vegetation, on oviposition site selection has rarely been experimentally studied to our knowledge. However, there have been some observational studies and field experiments that have examined this and related questions. Natural oviposition sites (i.e., pools, wetlands, ditches) of the rice frog (*Fejervarya*

limnocharis) had slightly higher vegetation cover (4 %) than sites not used for oviposition (Xu & Li, 2013). Oregon spotted frogs (*Rana pretiosa*) appear to prefer to oviposit in flooded wetlands that have had reed canary grass (*Phalaris arundinacea*) removed by mowing compared to control wetlands (Kapust et al., 2012). In a field study, ponds in which adult green and golden bell frogs (*Litoria aurea*) bred had more aquatic vegetation on average than ponds in which they did not breed (Klop-Toker et al., 2016). Glos et al. (2008) found that oviposition by *Aglyptodactylus laticeps* in artificial ponds was not affected by the presence or absence of leaf litter, but vegetative structure was not directly manipulated.

On its own, aquatic vegetation might be expected to affect the suitability of a habitat for tadpoles. Females may choose sites with more aquatic vegetation as it can have a positive effect on offspring success. For example, aquatic vegetation may increase the feeding rate and food consumption of tadpoles by affecting the profitability of the habitat, at least during some times of the day (Warkentin, 1992). In addition, the effects of a predator on oviposition might be mediated by the presence of vegetation or habitat structure. For example, the presence of aquatic vegetation can increase the survivorship of tadpoles in the presence of various invertebrate predators, possibly due to reducing the ability of predators to detect prey or by reducing capture success of the predator (e.g., Babbitt & Tanner, 1997, 1998; Tarr & Babbitt, 2002; Kopp et al., 2006; Cuello

et al., 2017). However, the efficiency of some tadpole predators is unaffected by vegetation cover, perhaps by providing the predator with a means of reaching their prey (e.g., crayfish, Figiel & Semlitsch, 1991; Chandler et al., 2016). Thus, the presence of vegetation, depending on how it might affect predation risk for tadpoles, may or may not affect oviposition site selection by adult anurans. The western mosquitofish (*Gambusia affinis*) is a widely introduced, invasive fish that has had significant negative effects on amphibian populations, primarily as a predator on their early aquatic life stages (review in Pyke, 2008). Hylids often avoid ovipositing in experimental ponds with *G. affinis*, presumably through detection of chemical or physical cues (e.g., Cope's gray treefrog, *H. chrysoscelis*, Binckley & Resetarits, 2003; gray treefrog, *H. versicolor*, Smith & Harmon, 2019, *Litoria aurea*, Pollard et al., 2017; western chorus frog, *Pseudacris triseriata*, Buxton et al., 2017). In addition, the presence of *G. affinis* in constructed wetlands negatively affected the abundance of *H. versicolor* (Shulse et al., 2013). This avoidance of ponds with *G. affinis* may be due to female frogs avoiding ovipositing in risky habitats since *G. affinis* are known to prey upon and greatly reduce the abundance of hylid tadpoles (Fryxell et al., 2015; Smith & Smith, 2015; Smith & Harmon, 2019). However, not all species of frogs appear to avoid ovipositing in habitats with mosquitofish. For example, Klop-Toker et al. (2018) found adult *Litoria aurea* at ponds with and without *Gambusia holbrooki*, but tadpoles were only found in ponds without *G. holbrooki*, suggesting that these adult frogs likely breed in both types of ponds (see also Klop-Toker et al., 2016).

The potential for aquatic vegetation to mediate the effect of *G. affinis* on oviposition site selection of anurans is not clear. Some studies found aquatic vegetation or habitat complexity reduced the ability of *Gambusia* to prey upon tadpoles (Morgan & Buttemer, 1996; Baber & Babbitt, 2004), even to the point of allowing coexistence (Preston et al., 2017). Thus, for adult anurans, the presence of aquatic vegetation might be a cue to lower predation risk for their offspring, and thus might affect their oviposition site selection. However, other studies found the presence of aquatic vegetation or habitat complexity had no effect on the injury rate (Shulse & Semlitsch, 2014) or consumption (Baber & Babbitt, 2004) of tadpoles by *Gambusia*. Indeed, *Gambusia* can be found in open water and in areas with submerged vegetation (Casterlin & Reynolds, 1977; Klop-Toker et al., 2018; review in Pyke, 2008), and *G. affinis* is found in both open water and vegetated habitats in local ponds (G.R. Smith & J.E. Rettig, unpubl. data), and are effective predators of tadpoles in both open or vegetated habitats, even if the vegetation does provide some refuge for tadpoles (Morgan & Buttemer, 1996; Baber & Babbitt, 2004). Thus, even though aquatic vegetation may provide some protection for tadpoles from predation by *Gambusia*, the effect of such predation is still potentially high enough to cause reduced abundances of tadpoles even in ponds with aquatic vegetation. Thus, it appears that the effects of aquatic vegetation on oviposition site selection by anurans may or may not be related to the presence of *G. affinis*.

We examined the effects of the presence of *G. affinis* and artificial vegetation on the oviposition site selection of free-ranging *H. versicolor*. *Hyla versicolor* is typically found in open marshes and in ponds with emergent vegetation (Collins & Wilbur, 1979). Vegetation cover positively affected *H. versicolor* tadpole abundance (Shulse et al., 2013), and appeared to reduce extinction probabilities of *H. versicolor*/*H. chrysoscelis* in wetlands, and may be important for egg deposition or as calling sites (Grant et al., 2018). However, the presence of aquatic vegetation in constructed wetlands had no effect on the abundance of *H. versicolor* in the presence of *G. affinis* (Shulse et al., 2013). *Hyla versicolor*/*H. chrysoscelis* may also be found in a range of pond hydroperiods from temporary to permanent ponds (Collins & Wilbur, 1979; Kiesecker & Skelly, 2001; Pauley, 2011). Mosquitofish readily colonise a variety of ponds and wetlands, including temporary ponds (Alemadi & Jenkins, 2008; see also Pyke, 2005). Indeed, we have observed *G. affinis* repeatedly colonise a local temporary pond after spring flooding, including ponds used by *H. versicolor* (G.R. Smith & J.E. Rettig, pers. observ.). Thus, *G. affinis* and *H. versicolor* potentially encounter each other in a variety of ponds where their distributions overlap. We predicted *H. versicolor* would avoid ovipositing in mesocosms with *G. affinis*. We also predicted greater oviposition by *H. versicolor* in mesocosms with vegetation. Given the apparent effects of vegetation on *G. affinis* predation on tadpoles in previous studies (see above), we predicted that the presence of vegetation would not affect avoidance of mesocosms with *G. affinis*.

MATERIALS AND METHODS

We used 32 Rubbermaid cattletanks (1136 L capacity; height = 63.5 cm, width = 175 cm, length = 160 cm) as experimental ponds. Our experiment consisted of a 2 x 2 factorial experiment in which the presence/absence of *G. affinis* and artificial vegetation were included as factors. Each treatment combination was replicated 8 times. We placed mesocosms in eight blocks of four mesocosms so that each treatment combination was present in each block. All blocks were placed at least 5 m apart within the same fenced area on the Denison University Biological Reserve, Granville, Licking County, Ohio. All mesocosms were filled with 800 L of well water to a depth of 44 cm (within the depth of local ponds used by these species) on 6 and 7 July 2013 and covered with 1 mm window screening to prevent colonisation by invertebrates and amphibians. On 8, 12, and 15 July, we inoculated all tanks with water (strained through 1 mm window screening) from nearby, natural ponds, and on 9 July 2013 we added 30 g of Rabbit Chow (Purina, St. Louis, MO) to introduce zooplankton and algae to the mesocosms and to facilitate algal growth. To ponds assigned to having vegetation present, we added submerged artificial vegetation in the form of lengths of nylon rope (40 cm long, 1 cm wide) and plastic aquarium plants (variety of "species"; Tetra, Blacksburg, Virginia, USA) weighed down with stainless steel nuts at the center of the mesocosm which provided a relatively dense vegetated area of rope and artificial

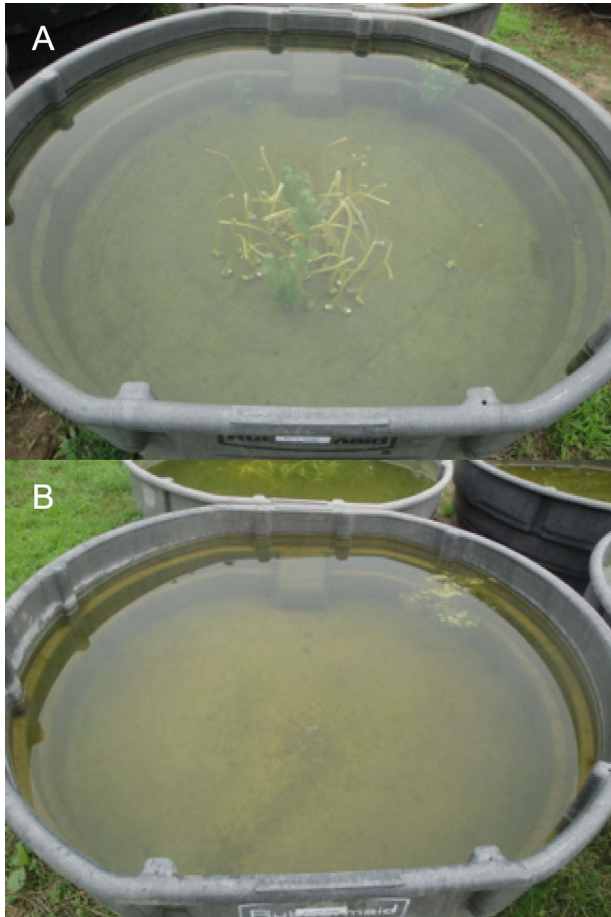


Figure 1. Photographs of representative mesocosms A) with artificial vegetation and B) without artificial vegetation..

plants through most of the water column (Fig. 1). The artificial aquatic vegetation “species” were chosen because they were similar in appearance and general structure to natural vegetation we have observed in local ponds, thus attempting to make the habitat more realistic. We used nylon rope to provide additional structure and density to supplement the artificial vegetation. To ponds assigned to having no vegetation present, we did not add either rope or artificial vegetation. We added 5 female *G. affinis* (45-55 mm total length) to each appropriate mesocosm on 18 July 2013 and removed the window screening to begin the experiment. The number of *G. affinis* added to the mesocosms is within the observed densities of *G. affinis* in local ponds (J.E. Rettig and G.R. Smith, unpubl. data).

Once the experiment began, we carefully searched each mesocosm for egg masses every morning shortly after sunrise from 19 July to 28 July. Our visual searching encompassed the entire surface of the water in each mesocosm, as well as the entire water column, the sides of the mesocosm, and the artificial vegetation (if present). We visually counted eggs using a hand-held counter. Female *H. versicolor* lay multiple clusters of eggs ranging in size from 30 to 40 (Cline, 2005), making counting eggs by eye easier than for other types of egg masses. We did not remove eggs from the mesocosms after counting. We were able to differentiate newly laid eggs from older eggs based on changes in the appearance of eggs and

their jelly coat, and only counted freshly laid eggs each morning. Embryo development (i.e., elongation) typically became obvious within 48-72 h after oviposition. Since mosquitofish are visual foragers (Russo et al., 2008 and references therein), and show a morning peak in foraging (Pyke, 2005), the opportunity for them to consume eggs before our morning egg surveys was limited. We never observed the fish consuming eggs during our daily checks. In addition, *G. affinis* do not consume *H. versicolor* eggs in our study population, only hatchlings and tadpoles (Smith & Smith, 2015). Therefore the egg counts we made are unlikely to have been affected by consumption of eggs by the fish. Allowing the eggs to remain in the mesocosms after counting could have affected the oviposition decisions of adult *H. versicolor* if they avoid potential competitors for their offspring (see Rudolf & Rödel, 2005; Schulte et al., 2011; Stein & Blaustein, 2015; Smith & Harmon, 2019). However, this is unlikely to have been very influential in our short experiment. In particular, the mesocosms did not appear to be saturated by eggs (e.g., some fishless mesocosms had not received eggs by the end of the experiment; see Results), and there were two cases when eggs were laid in mesocosms that already had eggs deposited earlier in the experiment. For mesocosms receiving eggs, we calculated the mean day of the experiment when eggs were deposited.

We used a two-way ANOVA to examine the effects of fish and vegetation treatments on the number of eggs laid in a mesocosm ($\log[x+1]$ transformed to meet the assumptions of parametric analyses). In a preliminary analysis the effect of pond block was not significant and thus has not been presented. We used JMP Pro 14.1 for all data analyses. Means are given ± 1 S.E.

RESULTS

We observed a total of 7,528 eggs in all mesocosms. We counted a total of 7,360 eggs in mesocosms with no *G. affinis* ($n = 16$ mesocosms) and 168 eggs in mesocosms with *G. affinis* ($n = 16$ mesocosms). A total of 3,850 eggs were deposited in mesocosm without artificial vegetation ($n = 16$ mesocosms) and 3,678 eggs were deposited in mesocosms with artificial vegetation ($n = 16$ mesocosms). We observed a total of 3,850 eggs in mesocosms with no *G. affinis* and no artificial vegetation ($n = 8$ mesocosms), 3510 eggs in mesocosms with no *G. affinis* and artificial vegetation ($n = 8$ mesocosms), zero eggs in mesocosms with *G. affinis* and no artificial vegetation ($n = 8$ mesocosms), and 168 eggs in mesocosms with *G. affinis* and aquatic vegetation ($n = 8$ mesocosms). We observed oviposition in three mesocosms with no *G. affinis* and no artificial vegetation, three mesocosms with no *G. affinis* and with artificial vegetation, no mesocosms with *G. affinis* and no artificial vegetation, and one mesocosm with *G. affinis* and with artificial vegetation.

There were significantly fewer *H. versicolor* eggs deposited in mesocosms with mosquitofish than were deposited in mesocosms without mosquitofish (Fig. 2; $F_{1,28} = 5.74$, $P = 0.024$). The presence of artificial vegetation had no effect on the number of *H. versicolor*

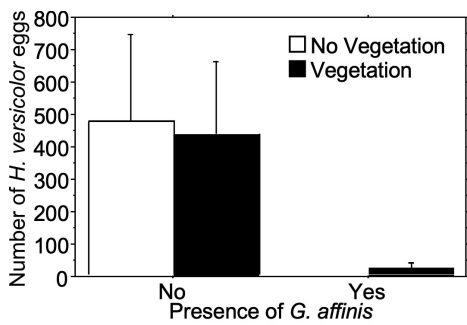


Figure 2. The effect of the interaction of the western mosquitofish (*Gambusia affinis*) and artificial vegetation treatments on mean (± 1 S.E.) number of gray treefrog (*Hyla versicolor*) eggs laid in mesocosms.

eggs deposited in a mesocosm (Fig. 2; $F_{1,28} = 0.11$, $P = 0.74$). There was no significant interaction between the mosquitofish and vegetation treatments (Fig. 2; $F_{1,28} = 0.11$, $P = 0.74$).

When considering only mesocosms in which oviposition occurred, eggs were laid on average on day 4.4 ± 0.8 of the experiment in mesocosms without *G. affinis* ($n = 6$) and on day 5 in mesocosms with *G. affinis* ($n = 1$). Eggs were laid on average on day 3.8 ± 0.6 in mesocosms without artificial vegetation ($n = 3$) and day 5.0 ± 1.1 in mesocosms with artificial vegetation ($N = 4$).

DISCUSSION

Our experiment demonstrates that *H. versicolor* avoid ovipositing in mesocosms with free-ranging *G. affinis*. The reduction in oviposition by *H. versicolor* in mesocosms with free-ranging *G. affinis* is consistent with other studies on anurans. *Hyla versicolor* and *H. chrysoscelis* avoid ovipositing in ponds with fish in general (Vonesh et al., 2009; Kraus & Vonesh, 2010; Kraus et al., 2011), and *G. affinis* and *G. holbrooki* specifically (Binckley & Resetarits, 2003; Smith & Harmon, 2019). The mechanism by which *H. versicolor* avoid *G. affinis* is unknown (i.e., is it due to detection of chemical or physical cues?). However, in another experiment, *H. versicolor* laid fewer eggs in the mesocosms with free-ranging *G. affinis* compared to mesocosms with caged *G. affinis* and laid eggs in mesocosms with caged *G. affinis* later than in mesocosms with no *G. affinis* (Smith & Harmon, 2019), suggesting both chemical and physical cues and likely resulted in the avoidance of *G. affinis* by ovipositing adults. The avoidance of *G. affinis* is likely adaptive since tadpoles of *H. versicolor* are readily consumed by *G. affinis* (Grubb, 1972; Smith & Smith, 2015) and few tadpoles persist in the presence of *G. affinis* (Shulse et al., 2013; Smith & Harmon, 2019). Thus, avoidance of ponds with free-ranging *G. affinis* is an example of risk-sensitive oviposition (Buxton & Sperry, 2017).

As far as we know, our study is the first to experimentally examine the effect of vegetation or habitat structure on oviposition site selection in *H. versicolor*. We found no evidence for its role in oviposition site selection, nor for a role for the interaction of

vegetation and predator presence. The lack of any effect of artificial vegetation/habitat structure on oviposition by *H. versicolor* in our experiment may arise because either the *H. versicolor* did not perceive the presence of the vegetation/habitat structure (i.e., not sufficiently realistic or not sufficiently abundant) or they did not perceive a benefit (or cost) from the vegetation/habitat structure, even though they are often found in ponds with aquatic vegetation in nature (e.g., Shulse et al., 2013; Grant et al., 2018). For example, vegetation structure had no effect on survival of larval *H. versicolor* in a mesocosm experiment in the absence of predators (Purrenhage & Boone, 2009), suggesting that aquatic vegetation on its own does not provide a benefit for tadpole survivorship in *H. versicolor*. In addition, the presence of aquatic vegetation in constructed wetlands does not appear to influence the abundance or presence of *H. versicolor*/*chrysoscelis* complex (Shulse et al., 2010). Thus, the presence of vegetation may not actually be a cue for a beneficial environment, at least relative to other cues.

We found no significant interaction between the presence of *G. affinis* and artificial vegetation on the number of eggs laid in mesocosms by *H. versicolor*, suggesting that the presence of the artificial vegetation did not mediate the effect of *G. affinis* on oviposition site selection by *H. versicolor*. However, *H. versicolor* did lay some eggs (total = 168 eggs) in mesocosms with both *G. affinis* and artificial vegetation, and none in mesocosms with *G. affinis* and no artificial vegetation. Thus, there may be a slight effect on oviposition site selection by *H. versicolor* but this is very minor relative to the contrast between the presence and absence of *G. affinis*. In addition, *G. affinis* tends to use submerged vegetation (Casterlin & Reynolds, 1977), and thus vegetation may also not provide any protection from *G. affinis*. For example, structural complexity did not affect or had minimal effects on predation rates on tadpoles (e.g., *Litoria aurea*, bleating tree frog, *Litoria dentata*, Morgan & Buttemer, 1996; squirrel treefrog, *Hyla squirrel*, Baber & Babbitt, 2004) or lower the injury rate of tadpoles (*Rana* spp., Shulse & Semlitsch, 2014) in the presence of *G. affinis*. In addition, the presence of aquatic vegetation in constructed wetlands had no effect on the abundance of *H. versicolor* in the presence of *G. affinis* (Shulse et al., 2013). However, the presence of aquatic macrophytes reduced predation of *G. affinis* on larval northern Pacific treefrog (*Pseudacris regilla*) in mesocosms which might explain how *P. regilla* coexisted with *G. affinis* in a lake experiment (Preston et al., 2017). Thus, 1) the presence of vegetation may not change the perception of predation risk due to *G. affinis* in a habitat or 2) the effects of the presence of vegetation on perceived predation risk by *G. affinis* may be variable and unpredictable, and thus may not be a useful cue for oviposition site choice in *H. versicolor*.

In conclusion, our experiment confirms the avoidance of fish, and more specifically *G. affinis*, by ovipositing *H. versicolor*. However, our experiment found no evidence for a role of vegetation/habitat structure in oviposition site selection in *H. versicolor*, whether on its own or mediating the effect of *G. affinis*, which suggests that

the presence of aquatic vegetation in ponds may not have benefits for the success of offspring. Our results therefore emphasise the necessity of maintaining wetlands, including temporary wetlands that *G. affinis* can colonise, free of non-native fish such as *G. affinis* to preserve viable populations of *H. versicolor*. Our results also suggest that submergent vegetation may not be used for initial oviposition site selection by *H. versicolor* and may not help mediate the negative effects of *G. affinis* on oviposition site selection. We recommend additional experiments on other species of amphibians, as well as experiments considering a range of fish densities and vegetation/habitat structure, especially experiments that use natural vegetation or that vary vegetation density or habitat complexity, to confirm or refine our results and conclusions.

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