Chapter 18
Detection of Fish and Newt Kairomones by Ovipositing Mosquitoes

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18.1 Introduction

Oviposition site choice is reproductive behavior in which oviparous organisms actively choose a habitat for their offspring based on its expected quality (Rausher 1983; Singer 1984). Many colonizing aquatic organisms with complex life cycles must choose between discrete aquatic habitats for their offspring, typically offering little parental care other than selecting a suitable oviposition site (Resetarits and Wilbur 1989). Since parental fitness depends on habitat quality, and the biotic and abiotic components of aquatic habitats can vary widely, selection should favor evolution of selective oviposition (Resetarits 1996). This is especially true for short-lived species such as insects since they have limited time to find a suitable oviposition site and may even only reproduce once (Blaustein 1999).

Selective oviposition has been documented in many aquatic insects (Chesson 1984; Petranka and Fakhoury 1991; Blaustein and Kotler 1993; Lowenberger and Rau 1994; Berendonk 1999; Resetarits 2001; Abjornsson et al. 2002; Binckley and Resetarits 2005) and amphibians (Resetarits and Wilbur 1989; Crump 1991; Kats and Sih 1992; Binckley and Resetarits 2002; Rieger et al. 2004; Vonesh and Buck 2007). Habitat choices are influenced by both abiotic (Bentley and Day 1989; Binckley and Resetarits 2007, 2008; Hocking and Semlitsch 2007) and biotic factors (Chesson 1984; Resetarits and Wilbur 1989; Petranka and Fakhoury 1991; Blaustein and Kotler 1993) that determine the potential quality of oviposition sites. The relative importance of these factors varies depending on the ecology and life-history of the species in question (Resetarits and Wilbur 1989; Berendonk 1999; Binckley and

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Resetarits 2007, 2008; Walton et al. 2009; Vonesh and Blaustein 2010). If individuals can reliably predict offspring performance, then selective oviposition will ultimately enhance parental fitness (Resetarits and Wilbur 1989; Blaustein et al. 2004; Hocking and Semlitsch 2007).

Mosquitoes, especially the genera *Culex* and *Culiseta*, offer a valuable model for studying oviposition site choice in response to predation because they meet criteria proposed by multiple authors (Rausher 1983; Singer 1984; Resetarits and Wilbur 1989; Resetarits 1996; Blaustein 1999): (1) egg-raft laying mosquitoes have few lifetime reproductive events, (2) they lay their eggs together in a clutch, and (3) their larvae are susceptible to predators. These three characteristics illustrate that a single, poor decision can lead to zero reproductive output. Also, predator characteristics may promote selective oviposition in prey, if predators are (4) heterogeneously distributed among patches, (5) remain in those patches during the prey larval period, and (6) reliably detectable (Resetarits and Wilbur 1989; Blaustein 1999; see also Blaustein et al. 2004). In addition, selectable patches must differ in a meaningful way in terms of predator distribution and abundance: if a predator is highly mobile, then selective oviposition may prove ineffective as a prey strategy. Given these criteria, one can predict which organisms should evolve selective oviposition in the context of effective, predictable predators.

It has long been assumed that semiochemicals, specifically kairomones, cued predator presence to ovipositing mosquitoes (Chesson 1984; Petranka and Fakhoury 1991; Angelon and Petranka 2002). A kairomone is an interspecific semiochemical released by an organism to the benefit of the receiver but not the emitter (Brown et al. 1970). Silberbush and Blaustein (2008) and Silberbush et al. (2010) established that ovipositing *Culiseta longiareolata* detect the presence of the predatory hemipteran *Notonecta maculata* via kairomones. A kairomone mechanism for fish deterrence has yet to be definitively established. Previous studies that suggested a kairomones mechanism had design issues, such as (1) using predators in cages (Petranka and Fakhoury 1991), which can still provide visual or tactile cues (Berendonk 1999), (2) using late instar larval counts instead of counting egg rafts, which is the only method to accurately assess oviposition choice (Petranka and Fakhoury 1991; Angelon and Petranka 2002), or (3) studying the interaction only with captive mosquitoes in artificial lab conditions (Van Dam and Walton 2008), which may not correlate with natural behavior (Bentley and Day 1989). We sought to improve upon these studies by definitively assaying natural mosquito oviposition in response to fish chemical cues.

Additionally, fish and notonectids have been used as model predators in 73 % of mosquito-predator oviposition research with 40 % of studies using only two species, the western mosquitofish (*Gambusia affinis*) and *Notonecta irrorata* (Vonesh and Blaustein 2010). However, other potential predators may affect mosquito oviposition. Central newts (*Notophthalmus viridescens louisianensis*) are aquatic salamanders that feed on mosquito larvae (DuRant and Hopkins 2008). They fill a similar role to small predatory fish in fishless habitats, and they function as keystone predators by preferentially feeding on superior competitors, thereby enhancing diversity (Morin 1981).

In this context, we wanted to answer two different questions: (1) Are kairomones alone responsible for fish avoidance during oviposition in *Culex* mosquitoes? (2) Do ovipositing *Culex* also avoid other predators during oviposition? In order to answer these questions, we conducted a series of three experiments using artificial pools to assay oviposition in natural mosquito populations.

18.2 Materials and Methods

18.2.1 Study Location

Our research was conducted at Tyson Research Center (795.8 ha) of Washington University located along the Meramec River in St. Louis County, MO. Tyson lies on the Ozark border and is comprised of oak and hickory secondary forest with sycamore, maple, and cottonwood in the bottomlands. It has patches of old fields and also a variety of permanent and temporary ponds and streams.

18.2.2 Fish Experiments

Two field experiments were conducted at Tyson during July–August 2013 to assay oviposition of natural mosquito populations. The experiments were constructed in two open fields with minimal tree canopy, 152 m apart. We constructed two separate arrays of black plastic tubs (66 × 45 × 16 cm), one array for each test species (16 pools place in eight pairs for each). All tubs were bleached, scrubbed, and power-washed between uses. Pools were separated by 1 m and each pair was 3 m from its nearest neighboring pair (Fig. 18.1). Pools were filled with tap water and left to age for 2 days. We then added 10 g of rabbit chow (Small World Rabbit Food—Mannapro, St. Louis, MO; 40 % protein) to facilitate pool detection.

Western mosquitofish (*G. affinis*) and green sunfish (*Lepomis cyanellus*) were selected for the experiment because they are native to Missouri and are both known predators of mosquito larvae (DuRant and Hopkins 2008; Silberbush and Resetarits *in prep*). Both species are opportunistic feeders that will also consume mosquito egg rafts (Eveland *personal observation*; Silberbush *personal observation*). Fish were collected from ponds at Tyson and kept in separate 1200 L holding tanks. Eight individuals of each fish species were haphazardly removed from their covered holding tanks and added to indoor 10 gal glass aquariums (51 × 28 × 30.5 cm) for 2 days. The fish were fed fish flakes (TetraMin® Tropical flakes—Tetra Holding inc., Germany) for the first 24-h then gut-cleared (no feeding) for an additional 48-h before being transferred to the pools. While in the pools, the fish had no access to food.

We used one predator species per array—western mosquitofish in one and green sunfish in another. In each array, we introduced a single fish to one pool in a pair that was randomly designated as the predator treatment. Each pool contained a cage that consisted of a black plastic plant pot with two screened sides (~1 mm mesh) and a screened lid. The fish were placed inside the cages of predator pools for 3 days and the pools covered to prevent any oviposition during the conditioning period. Before dusk on day 3, the fish were removed and the pools were opened to allow oviposition. All egg rafts were collected on the morning of day 4 and transferred to the laboratory. Egg rafts were individually hatched and larvae were reared to fourth instar and identified morphologically (Darsie and Ward 2005). The conditioning process was repeated four times for each site with different individual fish in the same pools.

18.2.3 Newt Experiment

From August 8th–14th we conducted a newt experiment at Tyson of much the same design as the fish experiments. We used eight pairs of the same type of plastic tubs with predator cages used in the fish experiments (Fig. 18.1). All tubs were cleaned in like manner as in the fish experiment. Each pool in a pair was separated by 0.91 m and pairs were dispersed over an area of 0.6 km^2. The minimum distance between two pairs was greater than 75 m. This design prevented interaction between pairs. All pools were positioned off dirt roads adjacent and parallel to the forest edge. The pools were filled with aged tap water and 5 g of rabbit chow (Small World Rabbit Food—Mannapro, St. Louis, MO; 40 % protein) was added to facilitate pool detection. Two randomly selected adult newts were introduced into the cage of one

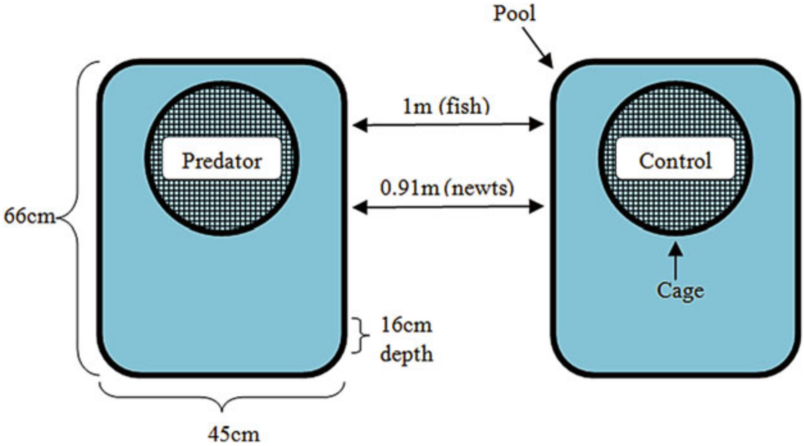

Fig. 18.1 The experimental design for all three experiments consisted of paired pools with cages. The fish experiments were conditioned with fish but only opened for oviposition when the fish were removed. The newt experiment contained caged newts. Newt pools were positioned 0.91 m (3 ft) apart and fish pools were separated by 1 m

randomly selected pool in each pair. The cage allowed the newts to interact with the water of the pool, but prevented prey consumption. Dead or consumed conspecific prey can produce cues that can potentially confound predator-released kairomones (Kats and Dill 1998). Curved plastic squares were placed in the cages to provide refuge for the newts. Unlike the previous experiment, newts were housed in the pools for the duration of the study, though it is unlikely they were visible or identifiable to species through the screen mesh. Pools were open for oviposition by natural mosquito populations. Since the pools were filled and had predators added on the evening on the same day, the first round of egg rafts were discarded without quantification. This was done in order to ensure mosquito oviposition took place only when the water was adequately conditioned with predator cue.

Egg raft collection and species identification mirrored that of the fish experiment, except egg rafts were collected daily since there was no conditioning period. The experiment was terminated after seven collection days, which was decided a priori because oviposition sharply declines after pools age for a week (Bohenek *unpublished data*; Bohenek and Silberbush *personal observation*). Newts were removed and weighed at the termination of the experiment in order to determine total predator biomass per pool.

18.2.4 Data Analysis

For each of the three experiments, we calculated a mean number of egg rafts per pool per day (daily average), which was square-root transformed [$\sqrt{}(x+0.5)$; (Yamamura 1999)]. We used paired, one-tailed Student's *t*-test to assess whether the daily average number of egg rafts laid in control pools was greater than predator pools. Lastly, a Pearson's product–moment correlation was performed for the newt experiment to determine if total newt biomass could predict the strength of the oviposition deterrence. Oviposition deterrence was calculated as the difference between the number of egg rafts in control pools and predator pools. All statistical analyses were performed in RStudio version 0.98.994.

18.3 Results

In total we collected 2006 egg rafts from our three experiments. A large sample from another experiment in the same study site was morphologically identified as *C. pipiens* complex (Barr 1957; Harbach 2012) and all (100 %) were subsequently identified using PCR as *C. pipiens* × *C. quinquifasciatus* hybrids (Silberbush and Resetarits *unpublished data*), hereafter "*C.* pxq." Our sample consisted of 75.12 % *Culex restuans* and 22.68 % *C.* pxq. Other species were ignored due to very low abundance (2.2 % of total).

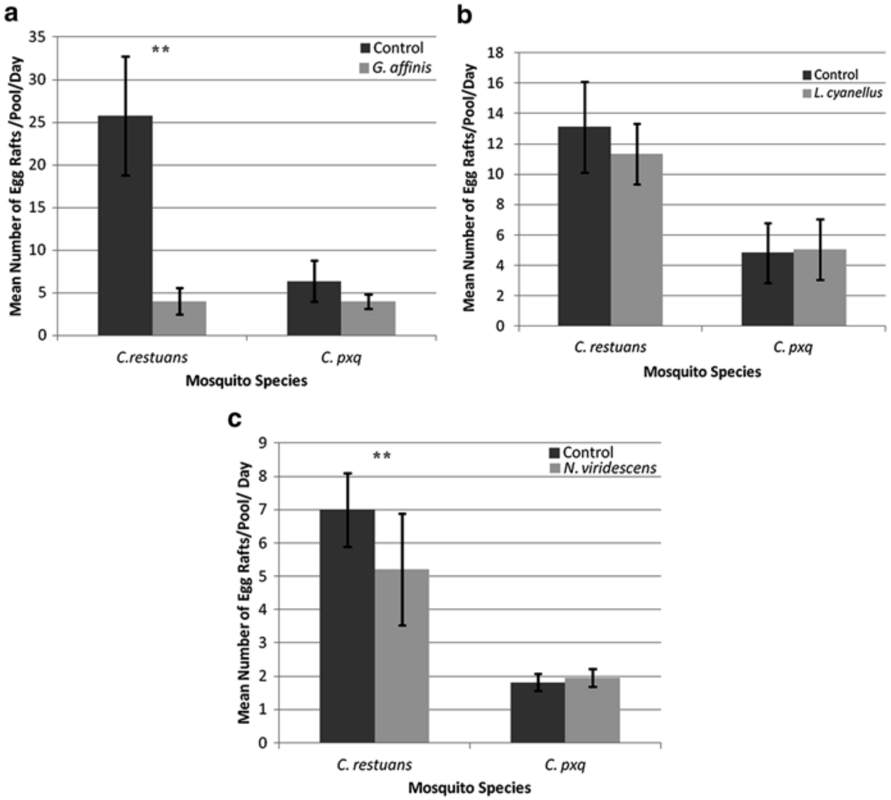

Fig. 18.2 Mean number (±SE) of egg rafts by mosquito species and predator treatment. The *dark gray bars* represent controls and the *light gray bars* represent predator pools with (**a**) western mosquitofish (*Gambusia affinis*), (**b**) green sunfish (*Lepomis cyanellus*) and (**c**) central newts (*Notophthalmus viridescens louisianensis*). $^{*}p<0.05$ and $^{**}p<0.01$

18.3.1 Fish Experiment

In the mosquitofish array, we collected 321 egg rafts; 238 (74.1 %) were *C. restuans* and 83 (25.8 %) were *C.* pxq. Mosquitofish had a significant effect on *C. restuans* oviposition ($t=4.00$, df $=7$, p-value $=0.0026$), with the mean number of egg rafts greater in the controls (Fig. 18.2a). Treatment had no effect on *C.* pxq oviposition ($t=0.71$, df $=7$, p-value $=0.25$). *C. restuans* laid 206 (87 %) egg rafts in the control pools and 32 (13 %) egg rafts in the mosquitofish pools. *Culex pipiens* laid 51 (61 %) egg rafts in the control pools and 32 (39 %) egg rafts in the mosquitofish pools.

There were two occurrences of fish mortality in the green sunfish array and the fish were immediately replaced. We collected 940 egg rafts; 692 (73.6 %) were *C. restuans* and 248 (26.4 %) were *C.* pxq. Green sunfish had no effect on the oviposition of either mosquito species—*C. restuans* ($t=1.15$, df $=7$, p-value $=0.14$) and *C.* pxq ($t=0.199$, df $=7$, p-value $=0.42$) (Fig. 18.2b). *C. restuans* laid 411 (59 %)

egg rafts in the control pools and 281 (41 %) egg rafts in the green sunfish pools. *C. pipiens*laid 128 (52 %) egg rafts in the control pools and 120 (48 %) egg rafts in the green sunfish pools.

18.3.2 Newt Experiment

We collected 913 egg rafts; 651 (71.3 %) were *C. restuans* and 149 (16.3 %) were *C.* pxq. One newt escaped from a pool, but the pool still contained the remaining newt. We detected a strong and significant species-specific response (Fig. 18.2c). Newts had a significant effect on *C. restuans* oviposition ($t = 3.298$, df = 7, p-value = 0.0066), but not on *C.* pxq oviposition ($t = -0.84$, df = 7, p-value = 0.79). *C. restuans* laid 384 (59.0 %) egg rafts in control pools and 267 (41.0 %) egg rafts in predator pools. *Culex* pxq laid 74 (49.7 %) egg rafts in control pools and 75 (50.3 %) egg rafts in predator pools. Pearson's product–moment correlation revealed no significant relationship between total newt biomass per pool (range: 3.53–6.11 g) and oviposition deterrence for *C. restuans* ($r = -0.500$; $t = -1.42$, df = 6, p-value = 0.21) or *C.* pxq ($r = -0.296$; $t = -0.759$, df = 6, p-value = 0.48).

18.4 Discussion

The detection and avoidance of predators by female mosquitoes when selecting an oviposition site is of critical importance to offspring survival and is the only parental care they offer. Oviposition behavior can affect species distributions, species interactions, offspring survival, and community structure (Resetarits and Wilbur 1989). Therefore, determining the mechanisms that mosquitoes use to detect predators aids in understanding the complex arms race between mosquitoes and aquatic predators. We focused on whether or not *Culex* mosquitoes can detect fish predators and central newts through predator-released kairomones.

Our results demonstrate that *C. restuans* use kairomones to detect and avoid western mosquitofish and central newts, but they do not avoid green sunfish. All three predator species are efficient consumers of mosquito larvae (DuRant and Hopkins 2008; Silberbush and Resetarits *in prep*). Predator efficiency depends on numerous factors such as availability of alternative prey and prey refuges (Webb and Joss 1997; Willems et al. 2005; Juliano 2009). Mosquitofish may have a greater impact on mosquito larvae compared with green sunfish resulting in greater selection pressure for detection of a mosquitofish kairomone. Western mosquitofish are tolerant of harsh abiotic conditions and are often found in large numbers (Offill and Walton 1999; Willems et al. 2005; Dam and Walton 2007; Walton 2007). A single mosquitofish can consume thousands of mosquito larvae in a 24 h period (DuRant and Hopkins 2008); thus, high numbers will most likely completely eliminate mosquito cohorts. Even when a mosquito is desperate to locate an oviposition site, it is probably more advantageous to continue searching than to settle for a habitat with mosquitofish. Alternatively, a few green sunfish might not necessarily have the same effect and can even be an indicator of reduced numbers of insect predators (Knight et al. 2005). Predator size may be another important factor since mosquitofish remain relatively small at adulthood compared to green sunfish. Mosquitofish may pose a constant predation threat while green sunfish predation on mosquito larvae occurs mainly in the smaller fish size classes. Mosquitofish and green sunfish may also forage in different microhabitats with mosquitofish favoring the water surface and green sunfish foraging lower in the water column and in the vegetation. Lastly, the pirate perch (*Aphredoderus sayanus*) is a freshwater fish that is not avoided by ovipositing *Culex* spp., nor by treefrogs and colonizing beetles, due to a form of chemical camouflage (Resetarits and Binckley 2013, Silberbush and Resetarits *in prep*). It is possible that green sunfish also possess some form of camouflage.

Despite considerable overlap in ecological niche, *C.* pxq and *C. restuans* vary in oviposition responses to predators. *C. restuans*, but not *C.* pxq, were selective, which was unexpected given that *C.* pxq also meet all criteria for evolving selective oviposition (Resetarits and Wilbur 1989; Resetarits 1996; Blaustein 1999). The simplest explanation is that *Culex* pxq may not be able to detect the predator-released kairomones in question, or require greater concentrations for detection. *Culex quinquefasciatus* has shown lack of mosquitofish cue avoidance (Walton et al. 2009) and *Culex* pxq has shown limited sensitivity (Angelon and Petranka 2002), so our results are not surprising. When considered from a life history standpoint, *Culex* pxq larvae may be more predator tolerant than *C. restuans* larvae. Or perhaps, *C.* pxq larvae are poor competitors, and thus risk predation in favor of reducing competition with *C. restuans* larvae. This tradeoff has been shown in damselflies where *Enallagma* species found in fish lakes were better able to avoid predation than species found in fishless lakes (McPeek 1990). Another possibility is that the hybrids have different behavioral algorithms than either pure species. It is typical for hybrids to display some intermediate behavior, even if it is maladaptive. Peach-face lovebirds (*Agapornis roseicollis*) transport nest-material by tucking it into their tail feathers while Fischer's lovebirds (*Agapornis fischeri*) carry nest-material in their beaks (Buckley 1969). Hybrids lovebirds display considerable difficulty choosing between a behavior and will repeatedly tuck and untuck nest-material in their tail feathers (Dilger 1962). Similarly, hybrid tree frogs (*Hyla* spp.) produce a vocalization that is intermediate between the parent vocalizations and less attractive to females (Gerhardt 1974). Similar chimeric behavior could limit the effectiveness of *C.* pxq behavioral responses. Aggression between ovipositing mosquitoes should also be considered since pool surface area is limited and *C. pipiens* will actively defend their oviposition site (Krause et al. 1992). If this aggression operates interspecifically, and *C. restuans* is superior in this respect, then *C.* pxq may be forced out of predator-free habitats. This variation between congeners demonstrates the potential for hidden complexity in life-histories that can determine community structure.

The detection and avoidance of fish is a potentially adaptive capability that can lead to a decrease in offspring mortality and an increase in reproductive success. Artificial lab studies have previously demonstrated that *C. tarsalis* (Van Dam and Walton 2008) and phantom midges (Berendonk 1999) use kairomones to detect predatory fish. Silberbush et al. (2010) found *C. longiareolata* detect predatory backswimmers (*N. maculata*) via predator-released kairomones when selecting an oviposition site. However, our field experiment is the first evidence of natural mosquito populations responding to fish kairomones. The next step is to identify the fish-released kairomones. Silberbush et al. (2010) identified n-tricosane and n-heneicosane as the chemicals *C. longiareolata* use to detect *N. maculata*. The responses to these hydrocarbons are also species-specific since *Anopheles gambiae* avoid *N. maculata*-conditioned water, but not water containing n-tricosane and n-heneicosane (Warburg et al. 2011). Thus, mosquito species may vary in their responses to specific kairomones and/or mixtures of kairomones and behaviors of specific mosquito species should not imposed onto other species, even if they are closely related.

Our results also describe the first evidence of adult amphibians deterring mosquito oviposition via kairomones. Newts are efficient predators of larval mosquitoes (DuRant and Hopkins 2008). Combining both oviposition deterrence and predation, newts can function similarly to mosquitofish in fish-free habitats but without the consequences attendant to fish introductions into previously fishless habitats (Hecnar and McLoskey 1997; Kats and Ferrer 2003; Schilling 2008). Not only can newts suppress mosquito populations, but they can even increase diversity in aquatic habitats due to their keystone predator effect (Morin 1981), thus providing a dual benefit over more generally destructive fish predators (Hecnar and McLoskey 1997; Kats and Ferrer 2003; Schilling 2008).

Given that newts were caged in the pools, the possibility of mosquitoes using tactile and/or visual cues instead of chemical cues remains. *C. pipiens* readily flees a water surface when disturbed (Schober 1966; Meillon et al. 1967). Since we observed an even number of *C.* pxq egg rafts between newt and newt-free pools, it is unlikely that any tactile or visual cues were sufficient to drive away ovipositing mosquitoes. This is true unless *C.* pxq responds differently than *C. restuans* to tactile or visual cues. Additionally, mosquitoes oviposit at night in shady areas and the predators were housed in cages that had three screened surfaces and two large opaque sides. Thus, visual cues seem unlikely especially since the newts often hid under a plastic refuge in each cage; however, an additional study using only newt cues may be worthwhile. The strength of newt deterrence was lower than that of mosquitofish. This could be due to a weaker chemical signature but also to predator behavior. Newts are lethargic when compared to constantly swimming mosquitofish, which should translate to lower kairomone production due to lower metabolic rates. Newt body mass was a negligible factor and fish biomass was not recorded, but mosquitofish we worked with at Tyson typically weigh less than 1 g, which is substantially less than mean newt biomass per pool (4.79 g; two newts per pool), while the green sunfish we worked with typically weighed 7–12 g. *C. restuans* avoided a single 1 g mosquitofish, but not a single 7–12 g green sunfish, which emphasizes the relative importance of predator identity over predator biomass. These findings are in accordance with past studies with fish that showed predator identity and its presence/absence are much more important than predator size and number, once a threshold for detection is reached (Rieger et al. 2004).

Since mosquitoes are an important disease vector (Gubler 1998; Gratz 1999), mosquitofish have been widely introduced as an attempt to biologically control their populations (Courtenay and Meffe 1989). However, fish introductions can dramatically degrade amphibian and invertebrate biodiversity (Hecnar and McLoskey 1997; Kats and Ferrer 2003; Schilling 2008). This is especially troublesome because many amphibian species are declining worldwide (Stuart et al. 2004) and fish introductions have been implicated as a major cause of declines in some species (Bradford 1989; Hecnar and McLoskey 1997; Knapp and Matthews 2000; Denoel et al. 2005). The potential efficacy of native wildlife as biocontrol agents has largely been ignored in favor of predators (often exotic) with known or presumed effects (Courtenay and Meffe 1989). Thus, characterizing predator-released kairomones in order to create natural, chemical mosquito oviposition deterrents and implementing the use of native predators (e.g., amphibian and insect predators) could lead to the control of disease vectors whilst reducing the deleterious effects of fish introductions. Semiochemicals are widely used in push-pull pest strategies where pests are spatially manipulated (Cook et al. 2007). In our system, kairomones act as a deterrent, which can *push* mosquitoes from a habitat of interest (e.g., temporary ponds near human populations). Whichever habitats the mosquitoes are pushed toward can then be managed to control populations with cryptic predators or other control methods.

It is now evident that mosquito congeners vary in their abilities to detect, or their predilection to avoid, predators and that not all predators are treated equally. The question remains as to how and why only certain mosquitoes would evolve avoidance of predators, especially since there is such adaptive potential for all mosquitoes. The answer may lie in the evolution of specific sensory capabilities, but it is also possible that predators are manipulating their own cues. This situation could result in an ongoing evolutionary arms race between predator and prey where mosquitoes are evolving finer sensory capabilities while predators are evolving different chemical signatures. For example, pirate perch (*A. sayanus*) are chemically camouflaged to oviposting treefrogs and colonizing beetles (Resetarits and Binckley 2013). It could be the case that newts and mosquitofish are currently ahead in the arms races with *C.* pxq, but behind in the race with *C. restuans*. In that context, green sunfish could be ahead with both mosquito species. In order to further understand the specificity of this system, we are currently investigating how the variation in predator effects could relate to phylogenetic signal and phylogenetic distance, as well as habitat use patterns. In addition, we plan on comparing the chemical signature of repellant predators to the non-repellant pirate perch in order to characterize predator kairomones. With the identification and proper implementation of a control strategy based on fish kairomones, mosquito populations may be controlled in such a way that minimizes the impact on resident aquatic biodiversity.

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