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Mosquito female response to the presence of larvivorous fish does not match threat to larvae

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Abstract. 1. Several species with complex life-history traits such as amphibians and insects with aquatic immature stages and terrestrial adults avoid ovipositing in pools containing larvivorous fish. This avoidance response was assumed to be a general one for most fish species.

2. The generality of ovipositing *Culex* to the presence of three, widespread larvivorous fish species was tested in a set of field experiments with artificial oviposition pools using caged fish.

3. Larval performance was further examined under actual predation by these three fish species.

4. Results show that ovipositing females responded strongly to the presence of caged mosquitofish, *Gambusia affinis*, while showing no significant response to the presence of caged green sunfish, *Lepomis cyanellus*, or the pirate perch, *Aphredoderus sayanus*. All three fish species consumed similar amounts of larvae.

5. This is the first example of species-specific response differences to predators during mosquito oviposition habitat selection. These results point to the existence of predator-released kairomones affecting mosquito behaviour. These kairomones may either be species-specific or vary in concentration among fish, and probably have an important role in the understanding of mosquito spatial distribution.

Key words. *Culex* mosquitoes, fish-released kairomones, habitat selection, larvivorous fish, oviposition, preference/performance.

Introduction

Predators can have lethal effects on prey individuals and populations either by direct consumption or indirectly by causing stressful reactions. In freshwater systems, predator presence is considered one of the major factors affecting species composition and prey distribution (Wellborn *et al.*, 1996; Knight *et al.*, 2005; Van Donk, 2007). Predatory fish are often top predators in these systems and have strong effects on a variety of invertebrates and amphibian populations (Wellborn *et al.*, 1996; Adler & Grunbaum, 1999; Knight *et al.*, 2005; (Van Donk, 2007); Weiss *et al.*, 2012).

Species with complex life histories, such as aquatic insects and amphibians, are subjected to different predation risks during the aquatic immature (egg, larval and, in some cases, pupal) and terrestrial adult stages. Many of these species provide little parental care beyond the selection of an offspring environment during oviposition, and the presence of predators in a small larval environment can strongly reduce the progeny. Therefore, we can expect strong selection favouring predator detection, and indeed, several species of amphibians and aquatic insects detect and avoid larval predators via oviposition habitat selection (Murphy, 2003); Rieger *et al.*, 2004; Brodin *et al.*, 2006; Blaustein & Whitman, 2009).

Understanding reactions of prey to the presence of different predators can shed light on the ability of prey species to manoeuvre in complex, multi-predator environments. However, most studies into the effects of cues from multiple predators on habitat selection either looked into each predator separately (Morosinotto *et al.*, 2010; Chobu *et al.*, 2015; Eveland *et al.*, 2016; Why *et al.*, 2016) or compared the response of prey to taxonomically remote (vertebrate versus invertebrate) predators (Turner *et al.*, 2000; Decaestecker *et al.*, 2002; Wesner *et al.*, 2012; but see Resetarits & Pintar, 2016).

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While different life-history strategies such as time and size at maturity and metamorphosis may be effective against different predators (Taylor & Gabriel, 1993; Higginson & Ruxton, 2010), predator avoidance, especially during oviposition or colonisation, usually involves similar responses (i.e. selecting a predator-free environment) that depend largely on predator recognition. This recognition may be species-specific for both prey and predator and is generally considered to depend on spatial overlap, predator efficiency, predictability and preferred habitat (Resetarits & Wilbur, 1989; Weiss *et al.*, 2012).

We tested the responses of ovipositing *Culex* mosquitoes to three species of predatory fish that are all effective predators of immature mosquitoes. Fish are known to have strong effects on mosquito populations and are often used as part of integrated pest management programmes (Bond *et al.*, 2005; Walton, 2007; Louca *et al.*, 2009). *Culex* species, in particular, breed in a large variety of water bodies and are likely to encounter larvivorous fish (Blaustein, 1992; Vinogradova, 2000; Becker *et al.*, 2010). There is, however, considerable interspecific variation in the ability of predatory fish to affect mosquito populations via consumption of larvae (Offill & Walton, 1999; Willems *et al.*, 2005) or competitive invertebrates (Van Dam & Walton, 2007).

This species-dependent variation in fish predation efficiency is reflected in larval life-history shifts of several mosquito species who alter time to pupation in addition to adult size and mass accordingly (Chobu *et al.*, 2015; Jourdan *et al.*, 2016). By contrast, responses of colonising tree frogs and aquatic beetles are similar, regardless of fish species' identity or effectiveness (Binckley & Resetarits, 2003; Resetarits & Binckley, 2013), with the exception of pirate perch, *Aphredoderus sayanus* Gilliams (Aphredoderidae) (Resetarits & Binckley, 2013; Resetarits & Pintar, 2016).

Here, we examine two hypotheses, assuming that ovipositing *Culex* respond to fish-released kairomones (Eveland *et al.*, 2016; Why *et al.*, 2016): (i) females react with a generalised fish-avoidance behaviour, as observed in tree frogs and beetles; and (ii) females' responses are species-specific and vary between fish species. These responses should reflect predator efficiency and produce a match between female preference and predator efficiency performance.

Methods

Oviposition site selection

Pools setups. Field experiments were performed at Tyson Research Center of Washington University, Saint Louis County, Missouri, using black plastic tubs of approximately 51 litres (66.04 × 50.8 × 15.24 cm) as oviposition pools, placed over 100 m apart from other potential oviposition sites to reduce distractions. Pools were filled to their maximum with water, and 17 g of rodent pellets (Small World Rabbit Food–Mannapro, St. Louis, Missouri; 40 % protein) were added to each pool to encourage oviposition. We placed a plastic cylindrical cage (28 cm in diameter with opening above the water surface) with all openings covered by a fibreglass screen at the centre of each pool. Pools were placed into positions in a ~25 × 15 m plot with ≥1 m between pools. Treatments (caged fish or fishless control pools) were randomly assigned within each set of three adjacent pools (block) containing two (caged) fish treatments and one fishless control pool; each of the experiments consisted of six such blocks ($n = 18$) and we assumed the ratio of one fish per 51 litres to be within the expected density in natural systems.

Data collection. Culex egg rafts, oviposited overnight, were counted and removed daily to reduce possible density-dependent effects, and pools were emptied and re-filled weekly in order to reduce temporal effects as much as possible (Chaves & Kitron, 2011). Larvae from collected egg rafts were reared to fourth instar, then identified morphologically using a Nikon SMZ800 according to Darsie and Ward (2005). Larvae morphologically identified as either *Culex pipiens* or *Culex quinquefasciatus* were further identified using DNA analysis (Appendix S1).

Fish treatments. As multiple choices can potentially reduce an observed effect (Rieger *et al.*, 2004; Silberbush *et al.*, 2010; Silberbush & Blaustein, 2011), we reduced the number of predator options by running three separate experiments, each with two fish species and a fishless control. The first, 20 June–18 July, with pools containing green sunfish, *Lepomis cyanellus* Rafinesque (Centrarchidae) and Western mosquitofish, *Gambusia affinis* Baird and Girard (Poeciliidae); the second, from 2 to 15 September with pools containing *A. sayanus* and *G. affinis*; and the third between 7 and 13 June the following year with pools containing *A. sayanus* and *L. cyanellus* (the first experiment was conducted over a longer time period due to low mosquito abundance in that particularly dry time period). All three fish species are known to feed on mosquito larvae (Parker & Simco, 1975; Blaustein, 1992; Walton, 2007) and to inhabit small, isolated pools with high levels of organic debris in that area (Pflieger *et al.*, 1975), which are probably breeding sites for *Culex*. Fish were collected from nearby sites, *G. affinis* and *L. cyanellus*, within a 5 km radius and *A. sayanus* from a site 65 km away [fish mass (mean ± SD ($n = 8$): *Lepomis*, 3.4 ± 0.49 g; *Gambusia*, 1.38 ± 0.31 g; *Aphredoderus*, 2.82 ± 0.66 g]. Fish were kept in 1200 litre holding tanks and rotated daily with the fish in the experimental pools, so a different fish (of the same species) was caged each day. Fish in the holding tanks were not given additional food and fed on invertebrate colonisers.

Predator efficiency

In order to investigate species-specific predator efficiency, we placed one fish, unfed for 48 h, of the same stock as those used in oviposition experiments in a 42.5 × 30.2 × 17.8 cm tub filled with ~10 litres of water. After another 24 h, 50 late-instar *Culex* larvae (collected from rain-filled pools and identified to Genera) were introduced to each tub. Larvae were counted after 1, 4 and 24 h. We repeated this in five temporal blocks, each containing the three fish species and a fishless control tub ($n = 20$). All counts were done during daytime (beginning ~10.00 hours) for technical reasons.

Data analysis

Field oviposition. We conducted separate univariate ANOVAS for each mosquito species in each of the three experiments. We summed all egg rafts of each species that were oviposited in each pool across all dates. We used the square root values of the summed number of egg rafts to improve homogeneity of variance, which we tested using Levene's test. We added 0.5 to the summed value to stabilise population variance (Yamamura, 1999). Block affect was not close to significance ($P > 0.33$) for all analyses except one (*Culex* p × q in Experiment 1), so the block effects were rolled into the error term for all but that single analysis. We used the Tukey–Kramer honest significant difference test (HSD) for pairwise comparisons.

Predator efficiency trials. We analysed the number of unconsumed larvae after the first and fourth hour using a one-way univariate ANOVA followed by Tukey–Kramer HSD, for pairwise comparisons. All analyses used STATISTICA 12 (StataCorp, 2011).

Results

Oviposition site selection

Two *Culex* species were sufficiently abundant for statistical analysis. *Culex restuans* Theobald was most abundant, comprising over 85% of total *Culex* egg rafts. Almost all remaining egg rafts were identified as *Culex pipiens-quinquefasciatus* hybrids, which will be referred to as *Culex* p × q (Appendix S1). We also found a few egg rafts of *Culex salinarius* Coquillett and *Culex tarsalis* Coquillett in numbers that were too low for biological significance. Other mosquito species found were *Aedes albopictus* Skuse, *Ochlerotatus japonicus* Theobald and *Anopheles punctipennis* Say. These species were not counted due to technical difficulties (i.e. single eggs, often stuck to the pool edge, are difficult to quantify). We found no invertebrate predator species and assumed no interspecific competition due to frequent water replacement. Although *Culex* p × q were less abundant than *C. restuans*, the two species showed a similar oviposition trend in all three field experiments. The first experiment (*Lepomis* and *Gambusia*) received a total of 415 *C. restuans* egg rafts, which varied significantly in distribution among treatments ($F_{2,17} = 7.45$; $P = 0.006$), with the mean number of egg rafts in control and *Lepomis* pools significantly higher than in *Gambusia* pools. *Culex* p × q oviposited a total of 78 egg rafts in this experiment and no egg rafts were found in *Gambusia* pools (Fig. 1a). Results varied significantly among treatments ($F_{2,17} = 5.48$; $P = 0.025$) with the mean number of egg rafts in control and *Lepomis* pools significantly higher than in *Gambusia* pools. In the second experiment (*Aphredoderus* and *Gambusia*), *C. restuans* again showed significant variation among treatments (75 egg rafts; $F_{2,17} = 18.45$; $P < 0.001$) with no egg rafts in *Gambusia* pools and a significantly higher number in both control and *Aphredoderus* pools. During this experiment, we found a single *C.* p × q egg raft in a *Gambusia* pool out of a total 27 egg rafts. This resulted in a marginally significant difference among treatments ($F_{2,17} = 3.39$; $P = 0.06$) with fewer egg rafts in *Gambusia* pools compared with the control (Fig. 1b). There were no significant differences in the distribution of *C. restuans* egg rafts among treatments in the third experiment, although the large number of egg rafts in *Aphredoderus* compared with *Lepomis* pools resulted in a nearly significant difference (363 egg rafts; $F_{2,17} = 2.8$; $P = 0.09$). Similarly, *C.* p × q egg rafts did not vary significantly among the treatments during this experiment (15 egg rafts; $F_{2,17} = 0.94$; $P = 0.41$), (Fig. 1c).

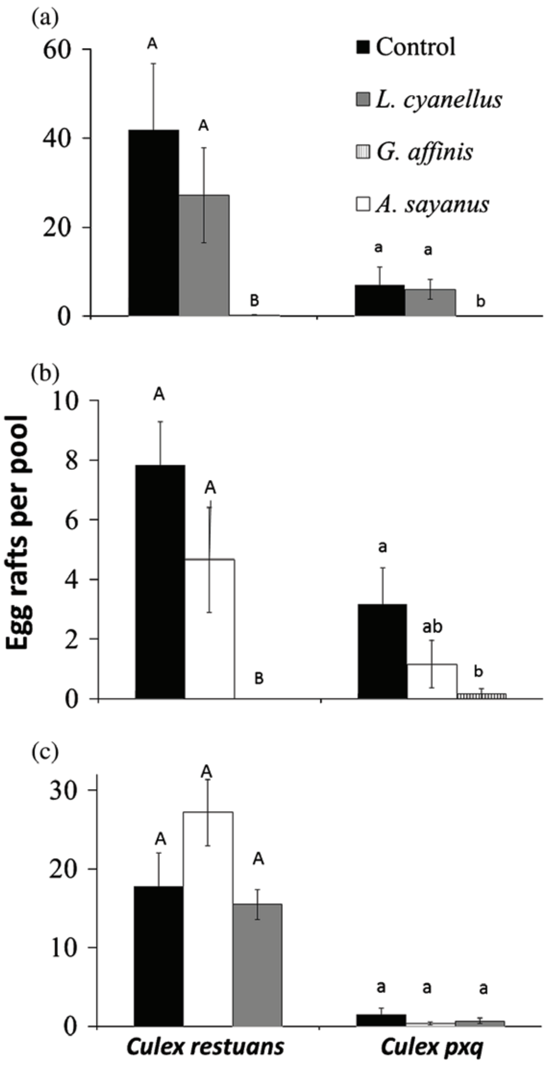

Fig. 1. Oviposition of *Culex restuans* and *Culex* p × q in the three field experiments: (a) *Lepomis* and *Gambusia*; (b) *Aphredoderus* and *Gambusia*; (c) *Aphredoderus* and *Lepomis*. Numbers are mean number of egg rafts per pool (±1 SE). Significant differences for *post hoc* pairwise comparisons (Tukey–Kramer honest significant difference test) are illustrated by upper- and lower-case letters for the separate analyses performed on *Culex restuans* and *Culex* p × q, respectively.

Predator efficiency

All fish began consuming larvae during the first hour ($F_{3,19} = 47.2$; $P < 0.001$). *Lepomis cyanellus* and *Gambusia*

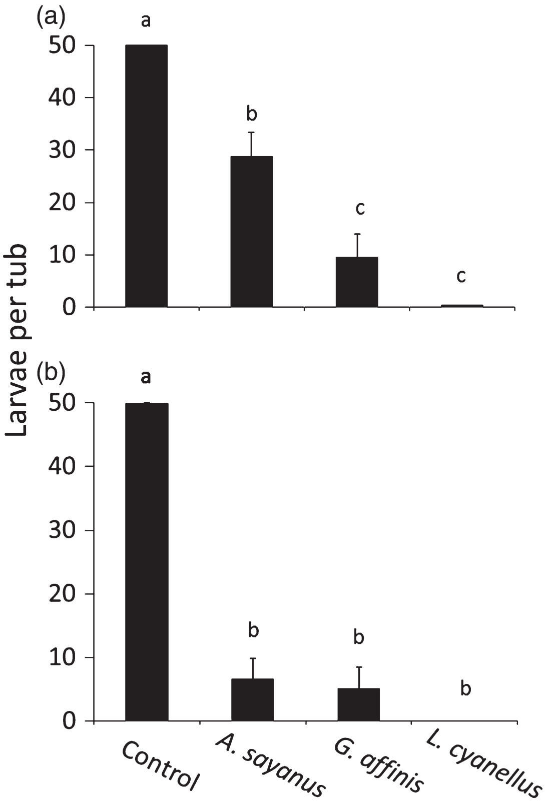

Fig. 2. Numbers of unconsumed larvae after 1 h (a) and 4 h (b). Numbers are means + 1 SE of unconsumed larvae per tub. Significant differences for *post hoc* pairwise comparisons (Tukey–Kramer honest significant difference test) are illustrated by lower-case letters.

affinis consumed a significantly higher number of larvae than *Aphredoderus sayanus* (Fig. 2a). After 4 h, however, we did not find a species-specific fish effect on the number of consumed larvae ($F_{3,19} = 100.67$; $P < 0.001$) (Fig. 2b). No larvae remained in fish treatments after 24 h, and there was no mortality in the controls during this period.

Discussion

How fine scale is the discrimination among predators by ovipositing mosquitoes? Fish are clearly the dominant predators in many aquatic habitats, and the ecological transition between fish and fishless habitats is one of the most dramatic in freshwater systems (Wellborn *et al.*, 1996; Knight *et al.*, 2005). Ovipositing tree frogs and colonising beetles show little discrimination among fish species, strongly avoiding species as different in predatory capabilities as fathead minnows (*Pimephales promelas*) and redfin pickerel (*Esox americanus*) (Resetarits & Binckley, 2013). In aquatic systems, predator detection is often achieved via chemical cues (predator-released kairomones) that travel better in water than visual or audio cues. Kairomones typically have a certain degree of volatility and small amounts can be detected from relatively long distances as well as from outside the water (Rieger *et al.*, 2004; Silberbush & Blaustein, 2008; Weiss *et al.*, 2012; Resetarits & Silberbush, 2016). Several species of aquatic predators are known to be detected by colonising prey via kairomones, including backswimmers (Silberbush *et al.*, 2010), predatory beetles (Ohba *et al.*, 2012) and fish (Brodin *et al.*, 2006; Weiss *et al.*, 2012; Resetarits & Binckley, 2013; Eveland *et al.*, 2016; Resetarits & Pintar, 2016). Ovipositing tree frogs and aquatic beetles respond to kairomones released by fish whose density (mass) is often >1 g in 100 litres of water (Rieger *et al.*, 2004; Binckley & Resetarits, 2005; Brodin *et al.*, 2006; Resetarits & Binckley, 2013). However, ovipositing mosquitoes are known to possess more sophisticated chemosensory apparatus (Clements, 1999), so there is potential for finer scale discrimination of both predator density (Silberbush & Blaustein, 2011) and species identity (Eveland *et al.*, 2016; Why *et al.*, 2016).

In our study, ovipositing *Culex* distinguished between different fish species rather than showing a general repellency affect. However, this response did not seem to match larval performance as all three fish species consumed similar amounts of larvae. The fact that *A. sayanus* initially consumed fewer larvae than the other species can most likely be explained by the primarily nocturnal activity of this species (Parker & Simco, 1975). Fish detection during oviposition was most likely a result of either variation in specific chemical signature or variation in concentration of cues. Future studies should look into the source and identity of these fish-released kairomones whose impact on colonising mosquitoes extends beyond the focal pool (Resetarits & Silberbush, 2016) and which also have strong impacts on larval development (Chobu *et al.*, 2015; Jourdan *et al.*, 2016).

While species-specific differences in larvae consumption by different fish could be shown in small water volumes without refuge (Homski *et al.*, 1994; Bhattacharjee *et al.*, 2009; Griffin, 2014; Chobu *et al.*, 2015), we cannot rule out the possibility that predation efficiency can differ in complex environments between the fish species in our study. We can, however, based on our results, assume that in smaller pools (resembling mosquito oviposition sites) even a small number of these fish are likely to consume an entire progeny before metamorphosis. Long-term effects on larval populations in pools inhabited by each of the three fish species are probably more complicated. For example, mosquito larvae, specifically *Culex*, often breed in highly polluted water where most fish do not dwell (Clements, 1999; Vinogradova, 2000; Becker *et al.*, 2010). However, *Gambusia* are able to withstand harsh conditions, such as high temperatures and low oxygen levels (Offill & Walton, 1999; Willems *et al.*, 2005; Van Dam & Walton, 2007; Walton, 2007). Therefore, water sources containing *Gambusia* are likely to be recognised and avoided by mosquito females. Because adult *L. cyanellus* and *A. sayanus* are primarily consumers of larger prey (Pflieger *et al.*, 1975), the presence of these fish might be an indicator of reduced numbers of invertebrate predators (Blaustein, 1992). However, this is probably only true in larger bodies of water, where *Gambusia* can also have a positive effect on mosquito larvae survival by consuming competitive species (Blaustein & Karban, 1990; Van Dam & Walton, 2007). In smaller pools, fish affect is probably more straightforward and additional tests of the interactive effects of fish species and water volume on oviposition and larvae survival can shed light on this issue.

Our study reinforces the role of fish-released kairomones in oviposition site choice and suggests that the nature of the kairomones may somehow allow discrimination among species. Avoidance cues from fish appear to be general rather than species-specific for ovipositing tree frogs and colonising beetles (Binckley & Resetarits, 2003, 2005; Resetarits & Binckley, 2013; Resetarits & Pintar, 2016). Avoidance responses have been shown to increase with predator lethality (Hoverman & Relyea, 2012) or show no relationship to lethality within a taxon (Resetarits & Binckley, 2013). Our results show a different oviposition reaction to three predatory fish that share habitat and a broad geographic range with the prey. Ovipositing *Culex* avoid *Gambusia* but show no response to *Lepomis* or *Aphredoderus*, despite similar overall levels of lethality. The question remains whether this is somehow an adaptive response by female mosquitoes to finer scale variation in predation risk or a simple consequence of recognition failure.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
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Appendix S1. Species identification.

References

Adler, F.R. & Grunbaum, D. (1999) Evolution of forager responses to inducible defenses. *The Ecology and Evolution of Inducible Defenses* (ed. by R. Tollrian and C. D. Harvell), pp. 259–285. Princeton University Press, Princeton, New Jersey.

Becker, N., Petric, D., Zgomba, M., Boase, C., Madon, M., Dahl, C. *et al.* (eds)SpringerLink (2010) *Mosquitoes and Their Control*. Anonymous. Springer, Berlin, Germany.

Bhattacharjee, I., Aditya, G. & Chandra, G. (2009) Laboratory and field assessment of the potential of larvivorous, air-breathing fishes as predators of culicine mosquitoes. *Biological Control*, **49**, 126–133.

Binckley, C.A. & Resetarits, W.J. Jr. (2003) Functional equivalence of non-lethal effects: generalized fish avoidance determines distribution of gray treefrog, *hyla* chrysoscelis, larvae. *Oikos*, **102**, 623–629.

Binckley, C.A. & Resetarits, W.J. Jr. (2005) Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. *Biology Letters*, **1**, 370–374.

Blaustein, L. (1992) Larvivorous fishes fail to control mosquitoes in experimental rice plots. *Hydrobiologia*, **232**, 219–232.

Blaustein, L. & Karban, R. (1990) Indirect effects of the mosquitofish *gambusia affinis* on the mosquito *culex tarsalis*. *Limnology and Oceanography*, **35**, 767–771.

Blaustein, L. & Whitman, D. (2009) Behavioral plasticity in response to risk of predation: oviposition habitat selection by a mosquito. *Phenotypic Plasticity of Insects: Mechanisms and Consequences* (ed. by D. Whitman and T. N. Ananthakrishnan), pp. 263–280. Science Publishers, Enfield, New Hampshire.

Bond, J.G., Arredondo-Jiménez, J.I., Rodríguez, M.H., Quiroz-Martínez, H. & Williams, T. (2005) Oviposition habitat selection for a predator refuge and food source in a mosquito. *Ecological Entomology*, **30**, 255–263.

Brodin, T., Johansson, F. & Bergsten, J. (2006) Predator related oviposition site selection of aquatic beetles (hydroporus spp.) and effects on offspring life-history. *Freshwater Biology*, **51**, 1277–1285.

Chaves, L. & Kitron, U. (2011) Weather variability impacts on oviposition dynamics of the southern house mosquito at intermediate time scales. *Bulletin of Entomological Research*, **101**, 633–641.

Chobu, M., Nkwengulila, G., Mahande, A.M., Mwang'onde, B.J. & Kweka, E.J. (2015) Direct and indirect effect of predators on *anopheles gambiae* sensu stricto. *Acta Tropica*, **142**, 131–137.

Clements, A.N. (1999) *The Biology of Mosquitoes. Volume 2: Sensory Reception and Behaviour*. Chapman & Hall, London, U.K.

Darsie, R.F. & Ward, R.A. (2005) *Identification and Geographical Distribution of the Mosquitos of North America, North of Mexico*. University Press of Florida, Gainesville, Florida.

Decaestecker, E., De Meester, L. & Ebert, D. (2002) In deep trouble: habitat selection constrained by multiple enemies in zooplankton. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 5481–5485.

Eveland, L.L., Bohenek, J.R., Silberbush, A. & Resetarits, W.J. Jr. (2016) Detection of fish and newt kairomones by ovipositing mosquitoes. *Chemical Signals in Vertebrates 13* (ed. by B. A. Schulte, T. E. Goodwin and M. H. Ferkin), pp. 247–259. Springer International Publishing: Imprint: Springer, Cham, Switzerland.

Griffin, L. (2014) Laboratory evaluation of predation on mosquito larvae by Australian mangrove fish. *Journal of Vector Ecology*, **39**, 197–203.

Higginson, A.D. & Ruxton, G.D. (2010) Adaptive changes in size and age at metamorphosis can qualitatively vary with predator type and available defenses. *Ecology*, **91**, 2756–2768.

Homski, D., Goren, M. & Gasith, A. (1994) Comparative evaluation of the larvivorous fish *gambusia affinis* and *aphanius dispar* as mosquito control agents. *Hydrobiologia*, **284**, 137–146.

Hoverman, J.T. & Relyea, R.A. (2012) The long-term impacts of predators on prey: inducible defenses, population dynamics, and indirect effects. *Oikos*, **121**, 1219–1230.

Jourdan, J., Baier, J., Riesch, R., Klimpel, S., Streit, B., Müller, R. *et al.* (2016) Adaptive growth reduction in response to fish kairomones allows mosquito larvae (*culex pipiens*) to reduce predation risk. *Aquatic Sciences*, **78**, 303–314.

Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A. & Holt, R.D. (2005) Trophic cascades across ecosystems. *Nature*, **437**, 880–883.

Louca, V., Lucas, M.C., Green, C., Majambere, S., Fillinger, U. & Lindsay, S.W. (2009) Role of fish as predators of mosquito larvae on the floodplain of the Gambia river. *Journal of Medical Entomology*, **46**, 546–556.

Morosinotto, C., Thomson, R.L. & Korpimäki, E. (2010) Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. *Journal of Animal Ecology*, **79**, 327–333.

Murphy, P.J. (2003) Does reproductive site choice in a neotropical frog mirror variable risks facing offspring? *Ecological Monographs*, **73**, 45–67.

Offill, Y.A. & Walton, W.E. (1999) Comparative efficacy of the three-spine stickleback (*gasterosteus aculeatus*) and the mosquitofish (*gambusia affinis*) for mosquito control. *Journal of the American Mosquito Control Association*, **15**, 380–390.

Ohba, S., Ohtsuka, M., Sunahara, T., Sonoda, Y., Kawashima, E. & Takagi, M. (2012) Differential responses to predator cues between two mosquito species breeding in different habitats. *Ecological Entomology*, **37**, 410–418.

Parker, N.C. & Simco, B.A. (1975) Activity patterns, feeding and behavior of the pirateperch, *aphredoderus sayanus*. *Copeia*, **1975**, 572–574.

Pflieger, W.L., Taylor, L. & Sullivan, M. (1975) *The Fishes of Missouri*. Missouri Department of Conservation, Jefferson City, Missouri.

Resetarits, W.J. Jr. & Binckley, C.A. (2013) Is the pirate really a ghost? Evidence for generalized chemical camouflage in an aquatic predator, pirate perch *aphredoderus sayanus*. *The American Naturalist*, **181**, 690–699.

Resetarits, W.J. Jr. & Pintar, M.R. (2016) Functional diversity of non-lethal effects, chemical camouflage, and variation in fish avoidance in colonizing beetles. *Ecology*, **97**, 3517–3529.

Resetarits, W.J. Jr. & Silberbush, A. (2016) Local contagion and regional compression: habitat selection drives spatially explicit, multiscale dynamics of colonisation in experimental metacommunities. *Ecology Letters*, **19**, 191–200.

Resetarits, W.J. Jr. & Wilbur, H.M. (1989) Choice of oviposition site by *hyla chrysoscelis*: role of predators and competitors. *Ecology*, **70**, 220–228.

Rieger, J.F., Binckley, C.A. & Resetarits, W.J. Jr. (2004) Larval performance and oviposition site preference along a predation gradient. *Ecology*, **85**, 2094–2099.

Silberbush, A. & Blaustein, L. (2008) Oviposition habitat selection by a mosquito in response to a predator: are predator-released kairomones air-borne cues? *Journal of Vector Ecology*, **33**, 208–211.

Silberbush, A. & Blaustein, L. (2011) Mosquito females quantify risk of predation to their progeny when selecting an oviposition site. *Functional Ecology*, **25**, 1091–1095.

Silberbush, A., Markman, S., Lewinsohn, E., Bar, E., Cohen, J.E. & Blaustein, L. (2010) Predator-released hydrocarbons repel oviposition by a mosquito. *Ecology Letters*, **13**, 1129–1138.

StataCorp (2011) *Stata Statistical Software: Release 12*. StataCorp LP, College Station, Texas.

Taylor, B. & Gabriel, W. (1993) Optimal adult growth of daphnia in a seasonal environment. *Functional Ecology*, **7**, 513–521.

Turner, A.M., Bernot, R.J. & Boes, C.M. (2000) Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. *Oikos*, **88**, 148–158.

Van Dam, A.R. & Walton, W.E. (2007) Comparison of mosquito control provided by the arroyo chub (*gila orcutti*) and the mosquitofish (*gambusia affinis*). *Journal of the American Mosquito Control Association*, **23**, 430–441.

Van Donk, E. (2007) Chemical information transfer in freshwater plankton. *Ecological Informatics*, **2**, 112–120.

Vinogradova, E.B. (2000) *Culex Pipiens Pipiens Mosquitoes: Taxonomy, Distribution, Ecology, Physiology, Genetics, Applied Importance and Control*. Pensoft Publishers, Sofia, Bulgaria.

Walton, W.E. (2007) Larvivorous fish including *gambusia*. *Journal of the American Mosquito Control Association*, **23**, 184–220.

Weiss, L., Laforsch, C. & Tollrian, R. (2012) The taste of predation and the defences of prey. *Chemical Ecology in Aquatic Systems* (ed. by C. Brönmark and L. Hansson), pp. 111–126. Oxford University Press, New York, New York.

Wellborn, G.A., Skelly, D.K. & Werner, E.E. (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, **27**, 337–363.

Wesner, J.S., Billman, E.J. & Belk, M.C. (2012) Multiple predators indirectly alter community assembly across ecological boundaries. *Ecology*, **93**, 1674–1682.

Why, A.M., Lara, J.R. & Walton, W.E. (2016) Oviposition of *culex tarsalis* (diptera: Culicidae) differs on water conditioned by potential fish and insect predators. *Journal of Medical Entomology*, **53**, 1093–1099.

Willems, K.J., Webb, C.E. & Russell, R.C. (2005) A comparison of mosquito predation by the fish *pseudomugil signifier* kner and *gambusia holbrooki* (girard) in laboratory trials. *Journal of Vector Ecology*, **30**, 87.

Yamamura, K. (1999) Transformation using $(x + 0.5)$ to stabilize the variance of populations. *Researches on Population Ecology*, **41**, 229–234.

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