

The effect of predatory fish exudates on the ovipositional behaviour of three mosquito species: *Culex quinquefasciatus*, *Aedes aegypti* and *Culex tarsalis*

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Abstract. Three mosquito species, *Culex tarsalis* Coquillett, *Culex quinquefasciatus* Say and *Aedes aegypti* L. (Diptera: Culicidae), were examined in laboratory binary choice experiments to investigate whether fish exudates from the mosquitofish, *Gambusia affinis* (Baird & Girard) (Cyprinodontiformes: Poeciliidae), deter oviposition and whether the responses of these mosquito species to fish exudates in oviposition sites are consistent with the risk of predation from fish experienced by each species in their respective natural breeding habitats. *Culex tarsalis* was deterred significantly from egg laying by the presence of fish exudates in oviposition cups, consistent with high levels of predation by fish in natural breeding sites. Egg laying by *Cx quinquefasciatus* was slightly reduced in water with fish exudates, but was not consistently deterred by water conditioned by mosquitofish, consistent with the species' relatively low risk of fish predation in natural habitats. Oviposition by container-breeding *Ae. aegypti* was not deterred by the presence of fish exudates in oviposition cups, consistent with a low risk of predation by fish in natural habitats.

Key words. *Aedes aegypti*, *Culex quinquefasciatus*, *Culex tarsalis*, *Gambusia affinis*, biological control, chemical detection, predator avoidance, semiochemicals.

Introduction

Culicids have been investigated extensively to determine if chemicals emitted by various organisms, such as bacteria, plants, insects, copepods and amphibians affect oviposition site selection (Ikeshoji & Mulla, 1970; Osgood & Kempester, 1971; Kramer & Mulla, 1979; Chesson, 1984; Isoe *et al.*, 1995; Torres-Estrada *et al.*, 2001; Mokany & Shine, 2003; Zahiri & Mulla, 2004), but the effect of fish exudates on the choice of oviposition sites by female culicids has been rarely investigated, despite the long history and global use of fish as biological control agents for mosquitoes (Gratz *et al.*, 1996). Petranka & Fakhoury (1991) found that larval mosquito abundance in wading pools containing caged bluegill, *Lepomis macrochirus* Rafinesque (Perciformes: Centrarchidae) was lower than in wading pools without fish, but did not directly measure mosquito oviposition. Ritchie & Laidlaw-Bell (1994) found that the density of *Aedes taeniorhynchus* (Wiedemann) eggs near pools containing fish was reduced relative to egg density near pools lacking fish, but did not determine

if visual, physical or chemical detection of the fish caused the decrease in oviposition. Angelon & Petranka (2002) measured a decrease in the number of larval mosquitoes in wading pools that contained chemicals released by the mosquitofish *Gambusia affinis* (Baird & Girard), but oviposition was not measured and factors other than a chemical oviposition deterrent may have contributed to the differences in the very sparse larval mosquito populations among treatments. Although these studies suggest that egg-laying mosquitoes use chemical signals to detect fish, no controlled laboratory studies have been performed to test this hypothesis.

The present study investigated the effect of fish-conditioned water on mosquito oviposition site selection in the laboratory. Oviposition choice experiments were conducted with three mosquito species: *Aedes aegypti* L., *Culex quinquefasciatus* Say and *Culex tarsalis* Coquillett, each of which utilize different types of oviposition site. The yellow fever mosquito, *Ae. aegypti*, lays eggs individually on the sides of containers (Carpenter & LaCasse, 1955; Vezzani & Schweigmann, 2002) that are natural

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(e.g. tree holes) or man-made (e.g. jars, tyres and drainage dishes under flower pots) and unlikely to contain fish. The southern house mosquito, *Cx quinquefasciatus*, lays egg rafts in containers (e.g. cemetery urns) and comparatively large oviposition sites, such as underground drains in urban settings, and in organically enriched ponds (Bohart & Washino, 1978; Meyer & Durso, 1993). Fish do not occur in the smaller container habitats and are unlikely to be present in oviposition sites containing high amounts of organic matter, but may occasionally occur in some highly enriched environments where *Cx quinquefasciatus* larvae are found. The western encephalitis mosquito, *Cx tarsalis*, frequently lays egg rafts in inundated vegetation such as sumps, rice fields and wetlands (Bohart & Washino, 1978), where fish are often present. We tested the ovipositional behaviour of these mosquitoes in the presence of fish exudates from *G. affinis*, the most widely used biological control agent against mosquitoes (Gratz *et al.*, 1996).

Materials and methods

Mosquito colonies

Culex quinquefasciatus mosquitoes came from a laboratory colony (CqSyn 90) that was established from wild individuals collected in southern California in 1990 (Georghiou & Wirth, 1997). *Culex tarsalis* mosquitoes came from a colony derived from wild individuals collected at the Eastern Municipal Water District's demonstration constructed treatment wetland (San Jacinto, CA) in 2001. *Aedes aegypti* mosquitoes came from a laboratory colony at the University of California Riverside started in 2000 with eggs from Thailand.

Similar rearing methods were used for the three mosquito species. Larvae were reared in enamel pans under standard laboratory conditions (27 °C, 16: 8 h light: dark [LD] cycle with 1-hour dawn and dusk periods) and fed *ad libitum* on a mixture of ground rodent chow and brewer's yeast (3 : 1, v:v). Pupae were collected into 300-mL cups (Solo Cup Co., Chicago, IL) and placed in cages measuring 30 × 30 × 30 cm (model #1450B; Bioquip Products, Rancho Dominguez, CA). The adult mosquitoes were allowed to feed on a 10% sucrose and water mixture. Once each week, female mosquitoes were fed overnight on 2–5-day-old restrained chicks.

Test materials

Mosquito oviposition preference was tested using two water treatments. A treatment containing exudates of fish and associated microbes, which will be referred to as 'fish-conditioned water', was produced by holding five adult *G. affinis*, which had been fed TetraPond flaked fish food, in a bucket containing 10 L of aged tap water for 24 h to allow the fish to empty their guts. The fish were then placed into a different bucket containing 10 L of fresh tap water for 24 h. Following removal of the fish, this water was used to test the effect of fish chemicals on mosquito oviposition. The control treatment comprised 10 L of fresh tap water that was held for 24 h and aged simultaneously with the

test treatment water. This process was repeated so that 1-day-old water was provided to gravid mosquitoes on each day of the experiments.

Mosquito oviposition experiments

Culex quinquefasciatus. Sixty blood-fed female *Cx quinquefasciatus*, approximately 7–10 days old, were aspirated into each of four 30 × 30 × 30-cm cages (model #1450B; Bioquip Products) and provided with a 10% sucrose solution. Oviposition preferences were tested from 4 days after each bloodmeal. Gravid mosquitoes in each cage were presented with two white 300-mL cups (Solo Cup Co.), each containing 100 mL of the treatment or control water with ~1 cm of space between the water surface and the top of the cup. The cups were placed in the cages at 16.30 hours, 30 min before the 1-h dusk period in the LD cycle began. The cups were removed from the cages at 11.00 hours the following morning and the number of egg rafts in each cup was counted. The placement of the cups within the cages was randomized on day 1 and the position of each cup was switched each day for 3 days. The females were blood-fed again a week later, used in a second oviposition trial (i.e. at 17–20 days old) and then discarded. This experiment was replicated three times during 2006 ($n = 12$).

Aedes aegypti. As for *Cx quinquefasciatus*, two cages, each containing 60 blood-fed female *Ae. aegypti*, were used to assess the response of mosquitoes to fish exudates. The amount of water in each oviposition cup was reduced to 30 mL to facilitate the placement of 3-cm-high strips of filter paper along the perimeter of the inside edge of each cup. All other procedures remained the same as for *Cx quinquefasciatus*. Each group of females in a cage was used for two gonotrophic cycles over a 2-week period (i.e. at 7–10 days old and 17–20 days). This experiment was replicated twice ($n = 4$).

Culex tarsalis. The responses of *Cx tarsalis* females to fish exudates were examined using two cages, each containing 60 blood-fed females aged 7–10 days. Experimental protocols for the 3-day experiments were the same as for *Cx quinquefasciatus*. Female mosquitoes in a pair of cages were used for two gonotrophic cycles over a period of 2 weeks. Oviposition trials were repeated with females in a second pair of cages for two gonotrophic cycles ($n = 4$).

Data analyses

Data were analysed using SYSTAT Version 9.01 (SPSS Inc., Chicago, IL). Because oviposition water was replaced daily following a bloodmeal, each female mosquito chose between comparable treatments on each day of an experiment, so the number of egg rafts/cup (*Cx quinquefasciatus*, *Cx tarsalis*) or eggs/cup (*Ae. aegypti*) was summed across the 3 days in a trial for each cage and across trials where the same mosquitoes were used in repeated trials. A paired *t*-test was performed on the total

number (ln-transformed) of egg rafts or eggs in each treatment among replicate cages for each mosquito species. Chi-square test was carried out to compare the pattern of distribution of oviposition choice between the two treatments among the replicate cages for each mosquito species.

An ovipositional activity index (OAI) was calculated by cage across dates for each species where the activity index was given as: $(NT - NS) / (NT + NS)$; NT is the number of egg rafts or eggs laid in the test cups and NS is the number of egg rafts or eggs laid in the control cups (Kramer & Mulla, 1979). This index varies between -1 and $+1$ so that -1 represents complete preference for control cups, $+1$ represents a complete preference for test cups, and 0 represents no preference between the two treatments.

Results

Culex quinquefasciatus

The southern house mosquito laid significantly fewer egg rafts on water conditioned by fish than on aged tap water (Fig. 1); however, egg-laying females did not respond consistently to the presence of fish exudates in the oviposition cups across cages ($\chi^2 = 20.59$, d.f. = 11, $P < 0.04$). The number of egg rafts laid on water containing fish exudates was significantly fewer than laid on aged tap water ($t = 3.67$, d.f. = 11, $P < 0.004$). On average, the percentage of egg rafts laid on fish-conditioned water was $75 \pm 23\%$ (mean \pm standard deviation) of the number of egg rafts laid on control water.

The OAI indicated that fish chemicals are a weak deterrent to egg-laying *Cx quinquefasciatus* under laboratory conditions (Fig. 2). Across the replicates, 44% of *Cx quinquefasciatus* blood-fed females placed in cages laid egg rafts on control water. Only 32% of *Cx quinquefasciatus* females placed in cages laid egg rafts on water conditioned for 24 h with fish. Approximately

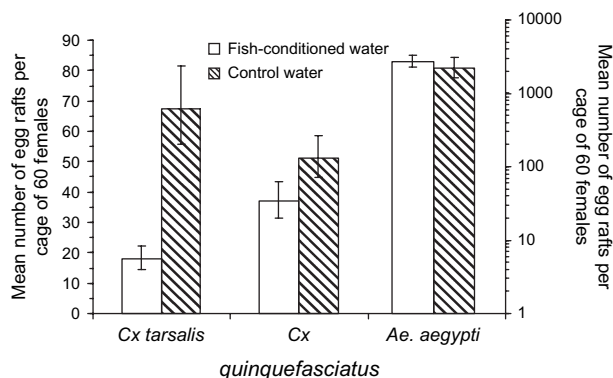


Fig. 1. Mean numbers of egg rafts laid per cage by *Culex tarsalis* (60 females/cage, $n = 4$ cages) and *Culex quinquefasciatus* (60 females/cage, $n = 12$ cages), and eggs laid per cage by *Aedes aegypti* (60 females/cage, $n = 4$ cages) in cups containing fish-conditioned water (five fish held in a 10-L bucket of tap water for 24 h) or aged tap water (10 L of tap water held for 24 h), averaged over two gonotrophic cycles. Back-transformed means \pm 95% confidence intervals are illustrated.

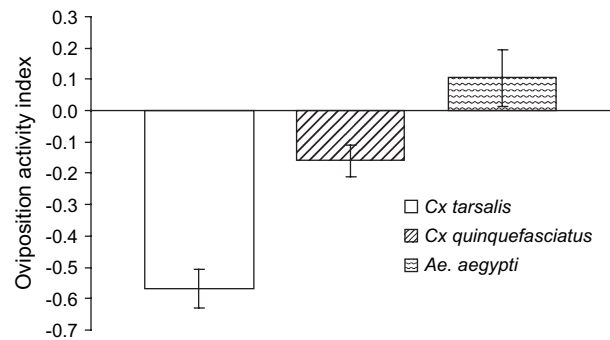


Fig. 2. Ovipositional activity index (mean \pm standard error) for *Culex* and *Aedes* species in response to water conditioned by the fish *Gambusia affinis*.

24% of female mosquitoes did not lay egg rafts during the experiments.

Aedes aegypti

The yellow fever mosquito did not respond to the presence of fish-associated chemicals in oviposition cups (Fig. 1). On a per cage basis, the number of eggs laid on fish-conditioned water did not differ significantly from the number laid on control water ($t = 1.43$, d.f. = 3, $P = 0.24$). In 50% of the trials, *Ae. aegypti* females laid appreciably more eggs on the edge of cups containing water conditioned for 24 h with fish than on the edges of cups containing aged water alone and oviposition choice was not homogeneous among the cages ($\chi^2 = 357.20$, d.f. = 3, $P < 0.001$). The OAI was slightly positive but indicative that female *Ae. aegypti* were not deterred from laying eggs in cups holding water conditioned by fish (Fig. 2).

Culex tarsalis

The western encephalitis mosquito responded strongly to the presence of fish-associated chemicals in oviposition sites ($t = 5.55$, d.f. = 3, $P < 0.012$). On average, four times (mean \pm standard error [SE] 4.3 ± 1.2 , $n = 4$) as many egg rafts were laid on control water compared with on water conditioned by fish (Fig. 1). Only 50% of females on average laid egg rafts during the trials; nevertheless, the number of egg rafts collected from oviposition cups containing control water vs. fish-conditioned water was consistent among the cages ($\chi^2 = 6.46$, d.f. = 3, $P > 0.09$). The average OAI index (mean \pm SE -0.57 ± 0.08) for these experiments showed a significantly higher repellence of mosquito oviposition by fish-conditioned water than in either of the other experiments using the other mosquito species (Fig. 2).

Discussion

Our experiments show that egg-laying females of the three mosquito species responded differently to fish-conditioned

oviposition cups, and the choice of oviposition cup made by mosquitoes of each species was consistent with the level of likelihood of that species encountering fish in its respective natural oviposition sites. Mosquito selection of oviposition sites can greatly influence individual fitness, population dynamics and community structure (Blaustein, 1999; Spencer *et al.*, 2002; Blaustein *et al.*, 2004). A wide variety of predator kairomones have been shown to benefit prey species survival in aquatic environments (Petranks & Hayes, 1998; von Elert & Pohnert, 2000; Binckley & Resetarits, 2003; Blaustein *et al.*, 2004), perhaps in part as a result of the ease with which the aquatic environment transmits chemical messages (Dodson *et al.*, 1994; Wisenden, 2000; Blaustein *et al.*, 2004). Mosquitoes use chemical and non-chemical cues detected in or around aquatic environments (Bentley & Day, 1989; McCall, 2002; Blaustein *et al.*, 2004) to avoid laying eggs in sites containing invertebrate predators (Tietze & Mulla, 1991; Stav *et al.*, 2000; Blaustein *et al.*, 2004). Non-chemical cues for predator detection are thought to be less valuable than chemical cues for selection of oviposition sites because of the often murky water and nocturnal conditions in which mosquitoes oviposit (Blaustein *et al.*, 2004).

Our results suggest that *Cx quinquefasciatus* is slightly repelled by fish-associated chemicals, but egg-laying females did not respond consistently across experiments to the presence of fish exudates in oviposition sites. *Culex quinquefasciatus* frequently oviposits in containers and isolated pools (Bohart & Washino, personal observation, 1978) and prefers water that has a high concentration of organic matter, such as can be found in cisterns (Bohart & Washino, 1978). Containers and polluted water are not habitats preferred by most fish species. Van Dam (2007) found that water enriched with organic matter and conditioned by *G. affinis* did not deter oviposition by *Cx quinquefasciatus* in the field and that increasing the density of fish by three times that used in the experiments reported here did not increase oviposition site avoidance by this mosquito in the laboratory. The difference in oviposition responses of *Cx quinquefasciatus* in the laboratory vs. the field may indicate that the effects of fish-associated chemicals on oviposition site choice in this species are dependent upon environmental conditions. Fish exudates may have a slight repellence in clean water but the attractiveness of volatiles produced by bacteria (Bentley & Day, 1989) in the organically enriched water used in field trials for ovipositing mosquitoes may have surpassed the slight deterrent effect of fish exudates. Regardless, from an evolutionary context, fish would not be a strong selective agent for a species that prefers containers and polluted water where fish are not frequently encountered.

The lack of a consistent measurable effect of fish-conditioned water on the choice of oviposition site for *Ae. aegypti* indicates that the presence of fish does not affect egg laying in this species. *Aedes aegypti* larvae are typically found in man-made containers and tree holes (Bohart & Washino, 1978; Bentley & Day, 1989; Vezzani & Schweigmann, 2002) and would not encounter fish on a regular basis. Therefore, *Ae. aegypti* might not be expected to reduce egg laying in the presence of fish-associated chemicals as a means of avoiding fish predation.

Selection for the ability to detect fish-associated chemicals by egg-laying *Cx tarsalis* is more likely than for the other two

species examined here and raises the question of just how important fish predation is as a selective pressure on culicid evolution. *Culex tarsalis* lays egg rafts in a wide variety of habitats (Bohart & Washino, 1978), many of which contain fish, and showed strong oviposition repellence to fish-conditioned water in laboratory experiments. Selection for the ability to detect the presence of fish occurs at the adult stage and may occur in other mosquito species that inhabit ecological niches similar to that of *Cx tarsalis*. Mosquitoes such as *Ae. aegypti* and *Cx quinquefasciatus*, which lay eggs in artificial and natural containers or utilize developmental sites that typically lack larvivorous fish, may rely on other ecological cues to select oviposition sites. Habitat size and location (e.g. whether it is above the ground or associated with trees) are likely to be important cues for egg-laying mosquitoes that use container habitats as developmental sites. Searching for sites that contain polluted water or other indicators of stagnant water may allow species with broad oviposition site preferences such as *Cx quinquefasciatus* to avoid habitats where fish are more abundant. Distinct odours given off by particular bacterial communities may be an important cue.

Oviposition sites that contain fish and sites that are fishless are not always adjacent in nature, as was the case in the binary choice experiments of this study. One exception is mangrove swamps (Ritchie & Laidlaw-Bell, 1994). Oviposition studies on *Aedes taeniorhynchus* suggest that fish exudates deter this species from ovipositing in small, isolated pools in mangrove swamps (Ritchie & Laidlaw-Bell, 1994).

Predator exudates have been shown to affect the larval behaviour and oviposition site selection of other mosquito species and other nematoceran Diptera. Even within the same ecosystem, prey species' responses to kairomones can be different depending upon the risk of predation. *Culiseta longiareolata* Macquart has been shown to avoid ovipositing in seasonal pools that contain notonectid kairomones (Eitam *et al.*, 2002; Blaustein *et al.*, 2004). Interestingly, chironomids whose larvae inhabited the same temporary pools as the *Culiseta* larvae did not show any oviposition deterrence to the notonectid chemicals, which may be related to their tendency to remain primarily in the sediments and are not heavily preyed upon by backswimmers (Blaustein *et al.*, 2004). Lake-dwelling species of chaoborid midges such as *Chaoborus flavicans* (Meigen) migrate to benthic regions from planktonic zones during the day to avoid fish predation in response to fish chemicals (Dawidowicz *et al.*, 1990; Tjossem, 1990). Other phantom midge species, such as *Chaoborus crystallinus* (Degeer), are rarely found in the presence of fish (Borkent, 1981). *Chaoborus* species inhabiting fishless lakes have not evolved the vertical migratory defensive mechanism in response to fish chemicals and thus cannot coexist with fish (Berendonk & O'Brien, 1996). Furthermore, females of *Chaoborus* species found in fishless lakes avoid ovipositing in water that contains fish chemicals (Berendonk, 1999).

Our experiments show that, for at least one species of adult dipterans with aquatic stages, the presence of potential larval predators affects ovipositional behaviour, and hence provides support for the hypothesis that increased sensitivity of egg-laying mosquitoes to fish exudates depends on the potential risk of predation in natal developmental sites. Experiments should be conducted to see if larval mosquitoes have also evolved

defensive mechanisms in response to fish exudates. Further experiments should be conducted to see if the results we obtained in the laboratory are consistent for the oviposition preferences of *Cx tarsalis* in nature. Results from such experiments might indicate that we need to reassess the importance of larvivory by *G. affinis* and other fishes in the biological control for mosquitoes. Finally, our findings show that the effects of fish-associated kairomones are not consistent across mosquito species, and that variations in response may be related to how closely a mosquito species is associated with habitats occupied by insectivorous fish.

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