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Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue

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Abstract Natural selection should favor females that avoid ovipositing where risk of predation is high for their progeny. Despite the large consequences of such oviposition behavior for individual fitness, population dynamics, and community structure, relatively few studies have tested for this behavior. Moreover, these studies have rarely assessed the mode of detection of predators, compared responses in prey species that vary in vulnerability to predators, or tested for the behavior in natural habitats. In an outdoor artificial pool experiment, we tested the oviposition responses of two dipteran species, *Culiseta longiareolata* (mosquito) and *Chironomus riparius* (midge), to the hemipteran predator, *Notonecta maculata*. Both dipteran species have similar life history characteristics, but *Culiseta longiareolata* larvae are highly vulnerable to predation by *Notonecta*, while *Chironomus riparius* larvae are not. As their vulnerabilities would suggest, *Culiseta longiareolata*, but not *Chironomus riparius*, strongly avoided ovipositing in pools containing *Notonecta*. An experiment in natural rock pools assessing oviposition by *Culiseta longiareolata* in response to *Notonecta maculata* yielded an oviposition pattern highly consistent with that of the artificial pool experiment. We also demonstrated that the cue for oviposition avoidance by *Culiseta longiareolata* was a predator-released chemical: *Notonecta* water (without *Notonecta* replenishment) repelled oviposition for 8 days. Oviposition avoidance and

mode of detection of the predator have important implications for how to assess the true impact of predators and for the use of commercially produced kairomones for mosquito control.

Keywords *Culiseta longiareolata* · *Chironomus riparius* · Kairomone · *Notonecta maculata* · Temporary ponds

Introduction

Numerous studies have documented a variety of induced responses by prey to risk of predation in aquatic systems (reviews in Chivers and Smith 1998; Kats and Dill 1998; Dicke and Grostal 2001). Only a surprisingly small fraction of these has considered oviposition decisions based on risk of predation to progeny (reviews in Blaustein 1999; Skelly 2001). Yet, such oviposition behavior may strongly affect individual fitness, population dynamics, and community structure (Blaustein 1999; Spencer et al. 2002). When oviposition habitat selection (OHS) in response to risk of predation has been documented, chemical detection of the predator has often been suggested as the likely cue (McCall 2002), but studies designed to test for this adequately are rare [aquatic systems: Berendonck (1999); Angelon and Petranka (2002); terrestrial systems: Grostal and Dicke (1999)]. Moreover, in the limited studies assessing this oviposition behavior, potential prey species that are predicted to exhibit OHS are usually tested while “unlikely” species, with rare exceptions (Berendonck and Bonsall 2002), are ignored.

Blaustein (1999) suggested that evolution of OHS in response to risk of predation is more likely when:

1. Progeny are highly vulnerable to the predator;
2. Prey have few lifetime reproductive events;
3. Eggs for each reproductive cycle are laid together as a single clutch and are not spread across multiple sites;
4. Predator density is highly heterogeneous among patches;

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5. Predator distributions among patches are highly fixed from the prey oviposition event until the prey progeny can either leave the patch or become large enough to be invulnerable to predation.

These criteria, particularly the fifth one, are more common in predator-prey systems of temporary pools than in terrestrial habitats (Blaustein 1999). All stages of microinvertebrate predators such as flatworms and cyclopoid copepods, and pre-metamorphic stages of insect predators and urodeles are confined to the pool from which they hatched or were born.

Almost all experimental studies assessing OHS in response to risk of predation in pool habitats have used artificial pools as their experimental venue (e.g., Chesson 1984; Resetarits and Wilbur 1989; Hopey and Petranka 1994; Blaustein et al. 1995; Resetarits 2001; Binckley and Resetarits 2002), with only a few exceptions using natural pools (Laurila and Aho 1997; Speiler and Linsenmair 1997). The reason for using artificial pools over natural ones is clear: ease of true and adequate replication (Wilbur 1997; Morin 1998; Blaustein and Schwartz 2001; Skelly and Kiesecker 2001). However, some studies assessing ecological interactions have shown that the outcome may differ in natural versus artificial pools. For example, Marsh and Borrell (2001) showed that, in an artificial pool experiment, the tungara frog strongly avoided ovipositing in pools containing conspecific egg masses and tadpoles, but in a natural pool experiment, no such pattern was detected.

Here, we compare the oviposition responses of two dipteran prey species, the mosquito *Culiseta longiareolata* Macquart (Diptera: Culicidae) and the midge *Chironomus riparius* Meigen (Diptera: Chironomidae), to risk of predation by a predatory backswimmer, *Notonecta maculata* Fabricius (Hemiptera: Notonectidae), and the mode of predator detection by the dipteran adults, if OHS occurs. We also experimentally determine if oviposition patterns exhibited in artificial pools are consistent with patterns in natural pools. The predator and prey species are common in temporary pools of Israel (e.g., Ward and Blaustein 1994; Blaustein and Margalit 1995; Blaustein 1998). *Notonecta maculata* nymphal instars are largely, if not completely, confined to the pool in which their eggs were oviposited. Adult *N. maculata* can remain in the same pool or disperse to other pools (Briers and Warren 2000). *Culiseta longiareolata* meets all of the criteria that Blaustein (1999) suggested for the likelihood of OHS in response to *N. maculata*. This mosquito lays all its eggs together as an egg raft. Immature development time (~2–3 weeks: Blaustein and Margalit 1994, 1996) is considerably shorter than the development time of the predator (~6 weeks). Immature *Culiseta longiareolata* are highly vulnerable to predation by *N. maculata* (Blaustein et al. 1995; Blaustein 1998). Mosquitoes generally experience high daily adult mortality (Service 1993), and thus only a small fraction survives to lay even one batch of eggs. *Chironomus riparius* has similar reproductive traits to those of *Culiseta longiareolata*; it has few reproductive

opportunities and it lays all its eggs in a cluster (Armitage et al. 1995). However, in contrast to *Culiseta longiareolata*, *Chironomus* larvae have low vulnerability to predation by *N. maculata* (Blaustein 1998). Consequently, we predicted that *Chironomus riparius* would not exhibit OHS in response to *N. maculata*.

In previous studies comparing equal numbers of pools containing *N. maculata* and not containing *N. maculata*, approximately 90% of the *Culiseta* egg rafts were observed in *N. maculata*-free pools (Blaustein et al. 1995; Blaustein 1998; Spencer et al. 2002; Kiflawi et al. 2003a). While OHS is the likely explanation of this distribution of egg rafts, these studies were not designed to eliminate alternative explanations, i.e., predation on either egg rafts or females alighting on the water to oviposit (Chesson 1984). The present study was designed both to differentiate between the OHS hypothesis and these alternative hypotheses, and to discriminate between chemical detection and other cues for detecting the predator. We show that OHS occurs as predicted relative to vulnerability to predation by the backswimmer, and that detection of the predator is via chemical cue. We also show that the pattern is consistent in two experimental venues: outdoor artificial and natural pools.

Materials and methods

Artificial pool experiment

We conducted an artificial pool experiment at Hai Bar Nature Reserve, Mt Carmel, northeastern Israel. Fourteen plastic tubs (0.6×0.4 m, 0.14 m depth; ~33.6 l) were placed in a 2×7 grid (inter-pool distance ~0.4 m) under a 90% shade net suspended at a height of 2 m. On 9 April 2000 we filled the tubs with tap water and added 14 cm³ of fish food pellets for nutrients. Water volume was maintained at ~13 cm depth (~31 l) with aged tap water. Seven pools were randomly assigned as control (no *N. maculata*) pools and seven as predator (*N. maculata*) pools. A cage, made from a 2 l plastic bottle containing three 50 cm² screen windows (mesh size 1 mm), was placed into, and removed from, each pool as described below. The cages in predator pools contained five *N. maculata* nymphs (instars IV–V) each while cages in control pools did not have *N. maculata*.

The experiment consisted of three phases. During the first phase, we placed the cages into the pools each morning (~08:00), removed them before sunset, and returned them the following morning. Because *Culiseta longiareolata* females oviposit at night, *Culiseta longiareolata* females searching for an oviposition site would thus not be exposed to the *N. maculata* themselves, but only to any possible chemical cues. Each morning, beginning when *Culiseta longiareolata* began ovipositing into these pools (11 April), we counted and removed mosquito egg rafts and chironomid egg strings. During this period (9 nights), we saved five randomly selected chironomid egg strings for hatching and subsequent identification of larvae: they were all identified as *Chironomus riparius*. *Chironomus riparius* egg strings were counted only during the first phase because they were rare afterwards. The removal of the predator cages after the ninth night marked the beginning of the second phase. In this second phase, to determine how long any potential predator-released kairomone repelled oviposition, the predator cages were left out of the pools while we followed *Culiseta* oviposition for 12 consecutive nights. In the third and last phase, we added three *N. maculata* (instar V) without the cages (we have found no difference in egg raft abundance in free versus caged

notonectid pools; (Eitam et al. 2002; Blaustein and Mangel, unpublished data) to each former predator pool and followed oviposition for 6 nights.

Natural pool experiment

We conducted a natural pool experiment in a linear array of ~40 m containing ten natural rock pools in Wadi Kelach, Mount Carmel, Israel, located about 2 km from the artificial pool experiment. Pool surface areas ranged from ~0.1 to 1.0 m² and maximum depths ranged from 6 to 21 cm. Because of the fairly large size range, we first paired pools of similar size (measured by surface area which was positively correlated with water depth: Pearson $r=0.71$; $P=0.05$), and then one pool from each pair was randomly assigned to the *N. maculata* treatment, and the other to the control. On 29–31 March 2000, we removed any predators that were detected in these pools. There were no *N. maculata* but there were fire salamander larvae (*Salamandra salamandra*) in most of the pools. Caged *S. salamandra* larvae do not elicit an oviposition avoidance by *Culiseta longiareolata* (Eitam and Blaustein, unpublished data) so we assumed that there would be no negative residual effect of *S. salamandra* on *Culiseta longiareolata* oviposition once this predator was removed. We then added fourth and fifth instar *N. maculata* nymphs at a density of one per 10 liters to those pools assigned to the predator treatment. Egg rafts that were found the next day were removed but not counted as part of the experiment: an a priori decision since there may not have been enough chemical accumulation of the predator. Beginning 2 April, we monitored egg raft deposition every 1–2 days. On 9 April, one pool was dry, and a second one was found to contain *S. salamandra* larvae (which can prey upon *Culiseta longiareolata* egg rafts: Blaustein, personal observation). Consequently, these two pools were excluded from the analysis. On 15 April, another pool had dried, so we ended our experiment with the previous observations on 13 April leaving us with oviposition counts for four control and four predator pools over 11 nights. During this period, we replaced any missing *N. maculata*.

Results

Artificial pool experiment

During the first phase, when ovipositing *Culiseta longiareolata* females could choose between control pools and pools that had contained *N. maculata* each day prior to, but not during, the oviposition time period, 92% (36 of 39) of *Culiseta longiareolata* egg rafts were oviposited into control pools (Fig. 1; binomial test: $P_{2tail} < 0.001$). During that same period, *Chironomus riparius* demonstrated no oviposition preference: 357 and 381 egg strings were deposited in control and *N. maculata* pools respectively (binomial test: $P_{2tail}=0.4$). The difference between the two species in their response to *N. maculata* was highly statistically significant (2×2 contingency table: $\chi^2=28.6$, $df=1$, $P_{2tail} < 0.001$).

During the second phase, when *N. maculata* were not returned to the pools during the day, the pools formerly containing the predator initially continued to repel *Culiseta* oviposition; over the first 8 days, 89% (92 of 104) of the egg rafts were found in control pools (Fig. 1; binomial test: $P_{2tail} < 0.001$). During the subsequent 4 days, only 58% (37 of 64) of the egg rafts were found in control pools. For a more formal analysis of the second phase, we used replicated G tests for goodness of fit (Sokal and

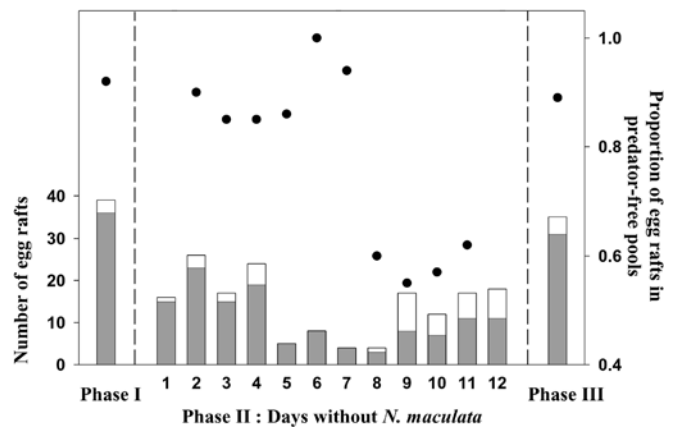


Fig. 1 Oviposition habitat selection by *Culiseta longiareolata* during the three phases. During phase I (9 nights), empty cages were placed in non-predator pools and caged *Notonecta maculata* were placed in predator pools during the day only but all cages were removed before sundown when *C. longiareolata* oviposits. During phase II (12 nights), *Notonecta* were not returned to their former pools and oviposition was checked each day. During phase III (6 nights), *Notonecta* were returned to the former *Notonecta* pools. Proportions of total number of *Culiseta longiareolata* egg rafts oviposited in non-predator pools for a specific time period are shown as dots. Each dot during phase II represents a moving mean of 3 consecutive nights. Numbers (histograms) of *C. longiareolata* egg rafts in non-*Notonecta* pools (shaded) and *Notonecta* pools (white) are for total periods in phases I and III and for each night of phase II

Rohlf 1995), dividing the data from the second phase into two sets: the first 8 days (set I), and the subsequent 4 days (set II). Both sets were homogenous with respect to the proportional use of control pools (set I: $G_H=5.95$, $df=7$, $P>0.25$; set II: $G_H=1.21$, $df=3$, $P>0.25$). The pooled data within each set was then tested against the proportional use of predator pools expected under random oviposition (i.e., 0.5). A statistically significant difference from the expected random oviposition (i.e., a significant OHS pattern) was observed in set I ($G_P=69.1$, $df=1$, $P<0.001$) but not in set II ($G_P=1.56$, $df=1$, $P>0.20$). It should be noted that the selection of set I and set II was based on post hoc examination of the data, and we predicted neither the duration of set I nor the abruptness of transition from set I to set II.

During the third phase, in which *N. maculata* was reintroduced to the former predator pools, oviposition preference for control pools returned (89%; 31 of 35 egg rafts; Fig. 1; binomial test: $P<0.001$).

Natural pool experiment

We analyzed the data as an analysis of covariance, where the response variable was the total number of egg rafts deposited in a given pool over the entire period, the independent nominal variable was *N. maculata* presence or absence, and the covariate was pool size (surface area). The model, including the interactive term, explained 96% of the variance in egg raft abundance where both *N. maculata* and pool size contributed significantly to the

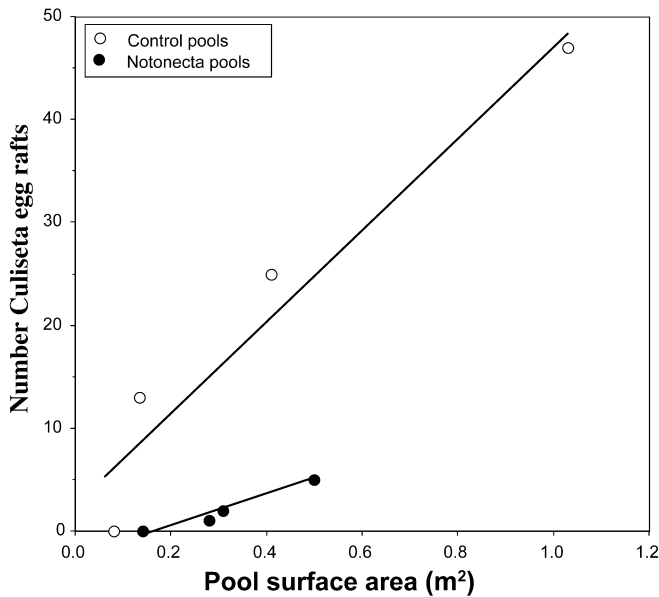


Fig. 2 Total *Culiseta longiareolata* egg rafts laid in each pool as a function of pool surface area and in the presence (closed circles) and absence (open circles) of the predator *Notonecta maculata* in the natural rock pool experiment. Best-fit lines for each category are shown

Table 1 Analysis of covariance model assessing the importance of pool surface area (covariate) and the presence/absence of *Notonecta maculata* in explaining variance in *Culiseta longiareolata* egg raft abundance across pools

Source of variation	df	Sum of squares	F ratio	P
Area	1	203.076	10.56	0.0314
<i>Notonecta</i>	1	475.196	24.71	0.0076
<i>Notonecta</i> ×area	1	53.526	2.78	0.1706
Error	4	76.915		

model (Table 1). Oviposition by *Culiseta longiareolata* was rare in the smaller pools regardless of whether or not they had *N. maculata*. Egg raft abundance increased with increasing pool size both in the presence and absence of *N. maculata*: over all pools, 91% (80 of 88) of the egg rafts were observed in control pools (Table 1; Fig. 2). Due to the deletion of two pools (one pool dried, the second pool was found to contain predatory fire salamander larvae) and the natural variation of pool sizes, the largest control pool was not matched by one of similar size in the *N. maculata* treatment. If we delete this large control pool from the analysis, both *N. maculata* and pool size remain statistically significant contributors ($P < 0.05$) to the model.

Discussion

To test predictions of which species should, and should not, respond to a predator when choosing oviposition sites, it is necessary not only to test those species expected to exhibit the oviposition behavior, but also to test those not

expected to do so. *Culiseta longiareolata*, which meets all conditions suggested to favor the evolution of OHS in response to *N. maculata* (Blaustein 1999), indeed exhibited the OHS response. *Chironomus riparius*, which does not meet the condition of high larval vulnerability to this predator (Blaustein 1998), did not avoid *N. maculata* when ovipositing. Similarly, *Chaoborus flavicans*, whose larvae are not highly vulnerable to predation by fish, does not avoid ponds containing these fish when ovipositing while *Chaoborus crystallinus*, whose larvae are highly vulnerable to these fish, avoids ovipositing in ponds containing the predatory fish (Berendonck and Bonsall 2002). To test the robustness of the predicted set of conditions suggested by Blaustein (1999) for a likely OHS response, many more tests are necessary in which both prey species that are highly vulnerable to predation, and those species not highly vulnerable, are included.

We found highly similar oviposition patterns in response to risk of predation in the natural and artificial pool experiments. Artificial pool experiments may not yield realistic ecological interactions in some cases (Skelly 2002). However, in the case of OHS, particularly when the cue is chemical, we suggest that finding similar results in artificial versus natural pools is not a validation of the use of artificial pools to test this behavior but an indication of the importance of this factor relative to other factors. For example, Marsh and Borrell (2001) found that tungara frogs avoid conspecific larvae and eggs in an artificial pool experiment but failed to find such an effect in a manipulation of conspecifics in natural pools. This does not bring into question that tungara frogs are incapable of detecting conspecifics and ovipositing accordingly. They did in fact demonstrate in the artificial pools that they have this ability. They interpret the absence of a detectable effect in natural ponds as other factors that vary across the natural ponds having overriding effects. The rock pools that we used for our natural pool experiment were the best set of pools that we could find in the area to serve as “replicates” for an experiment. Yet this set of rock pools did not provide nearly the consistent conditions among replicates as did the replicates of our artificial pool experiment: the natural rock pools varied greatly in size, which we attempted to compensate for statistically. But they varied greatly in many other factors. For example, they varied in pH (7.6 to 9.0), amount of sediment, and probably other factors that could potentially be important to a mosquito searching for a home for its progeny. We interpret the similarity of results between the natural and artificial pools as evidence that risk of predation is a very important factor, perhaps an overriding factor, in determining an oviposition site for this mosquito. That *Culiseta longiareolata* oviposited more in larger pools may be due to an increased probability of encounter with larger pools, or to preferential choice of larger pools.

We demonstrated that the mode of detection of *N. maculata* by *Culiseta longiareolata* was chemical. Although mosquito oviposition may be deterred by cues from predators that are not chemical (e.g., Tietze and

Mulla 1991; Stav et al. 2000), it is not surprising that *Culiseta longiareolata* utilizes a chemical cue for several reasons. First, chemical cues are used widely by aquatic prey to detect predators (e.g., Petranka and Hayes 1998). This is likely because aquatic environments provide a medium conducive to dispersal of chemicals and detection of them (Dodson et al. 1994; Wisenden 2000). Second, mosquitoes are known to have receptors for detecting a variety of chemicals in, or emanating from, water (Bentley and Day 1989; McCall 2002). Third, other modes of detection may not be particularly reliable in aquatic habitats: ovipositing mosquitoes in an air environment are unlikely to be able to visually detect predators well in an often murky aquatic medium, particularly at night, nor are they likely to be able to distinguish well between vibrational cues caused by predator movement and the vibrations caused by numerous other non-predaceous animals in the water.

This putative, but as yet unidentified kairomone, without replenishment, elicited strong oviposition avoidance for at least 1 week. Although chemical cues used by other aquatic prey species in response to risk of predation appear to be of shorter life, little work has been conducted on longevity of predator-released kairomones. Contributing to our lack of knowledge about the stability of predator-released kairomones are experimental designs which measure the absence of a prey response with increasing time but do not distinguish whether this lack of response is attributable to the breakdown of the chemical or habituation of prey to the predator (Wisenden et al. 1995). Turner and Montgomery (2003) controlled for habituation and found that predator (sunfish) water up to 4 days old elicited anti-predator responses by prey species (snails).

Unlike some prey species that respond to risk of predation only once conspecifics have been consumed (e.g., Laurila et al. 1998; Wisenden and Millard 2001), this chemical does not appear to be released as a result of consumption of *Culiseta longiareolata*: caged *N. maculata* were not fed *Culiseta longiareolata* larvae during the first week of the experiment.

Detection of a predator-released chemical by prey which is common across a wide taxonomic range of predators is likely to be beneficial to the prey (von Elert and Pohnert 2000; Binckley and Resetarits 2003). We have found similar OHS responses by *Culiseta longiareolata* to two additional caged notonectid species tested (*Anisops sardea*: Eitam et al. 2002; *A. coutierei*: Silberbush et al., unpublished). The cue elicited by these two *Anisops* species is probably also chemical and probably the same chemical elicited by *N. maculata*. A metabolic byproduct is a likely cue, as the evolutionary elimination of such a kairomone should be selected for if it were nonessential. This chemical may be common to all notonectids, but it is not common to all aquatic predators; caged odonates and caged urodeles (Stav et al. 2000; Eitam et al., unpublished data) do not elicit this OHS response in *Culiseta longiareolata*.

The consequences of OHS for population dynamics take on applied importance when the ovipositing species is a pest after metamorphosis. If the selective oviposition behavior exists but non-selective oviposition is assumed, and the effects of various predators on pest populations are assessed in an experimental design comparing pest abundance in predator versus non-predator plots, the real negative effect of the predator will probably be overestimated (Blaustein 1999; Spencer et al. 2002).

Kairomones, such as we infer to be at work in the backswimmer-mosquito system, if commercially produced, may provide an environmentally friendly chemical control. The applied chemical is more likely to affect mosquito abundance negatively if the mosquitoes persist in searching for a "good" oviposition site: the longer it searches, the higher the probability of mortality prior to ovipositing. When *Culiseta* females are experimentally offered only poor oviposition choices (sites containing predators or high densities of conspecific larvae), oviposition rates drop significantly (Kiflawi et al. 2003b). Moreover, if mosquito adults oviposit largely in the subset of the pools that do not have the kairomone, then intraspecific competition may increase, which could negatively affect the adult population. The relative importance of mortality during searching for an oviposition site and intraspecific competition after oviposition as factors contributing to adult mosquito population density remains to be investigated theoretically and empirically.

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