

# *Effects of predator type and alternative prey on mosquito egg raft predation and destruction*

**Shomen Mukherjee & Leon Blaustein**

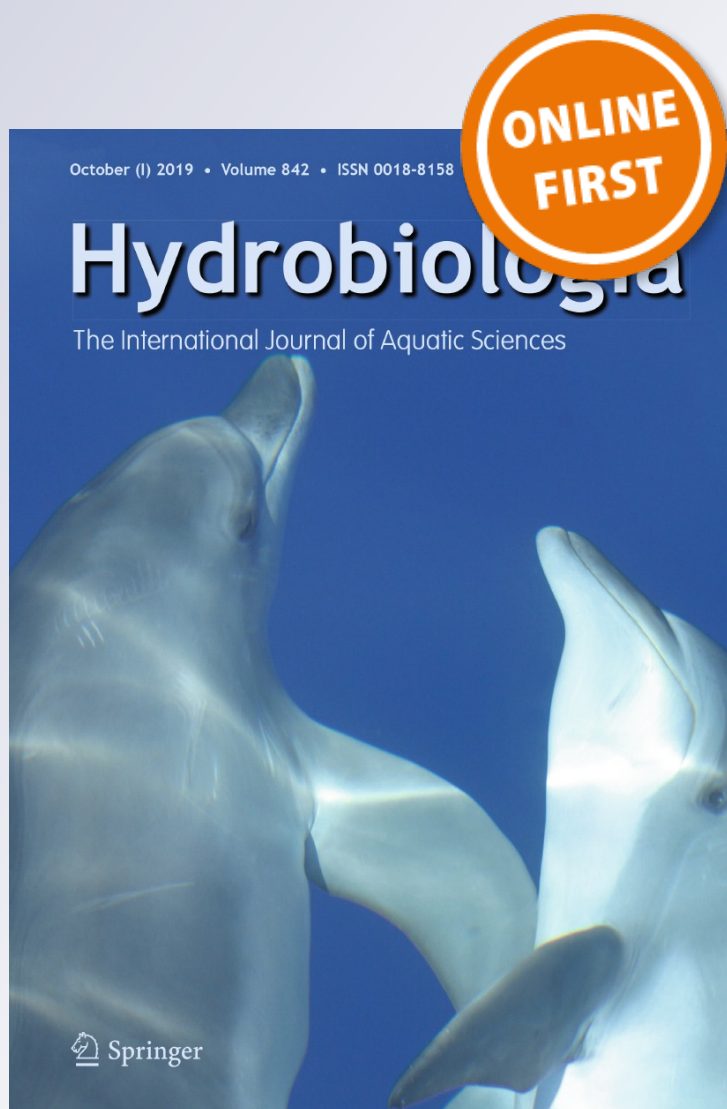
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## PRIMARY RESEARCH PAPER

# Effects of predator type and alternative prey on mosquito egg raft predation and destruction

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**Abstract** For a vector species, understanding their egg raft predation (consumption) or destruction is essential for both ecological and human health reasons since it directly influences its fitness. In a mesocosm experiment, we assessed differences in *Culiseta longiareolata* egg raft predation/destruction by three aquatic predators *Notonecta maculata* (backswimmers), *Sympetrum fonscolombii* (dragonflies) and *Ommatotriton vittatus* (newts), both in the presence and absence of an alternate prey (*Culex* larve). Egg raft predation and destruction significantly differed between predators types, and strongly influenced by the presence of alternate prey. Backswimmers attacked and destroyed (broke down) all egg rafts until they disintegrated and sank in water regardless of whether an alternative prey was present. Egg raft predation by dragonflies was common in the absence of alternative prey, but rare when alternative prey was present. Predation by newts was rare regardless of

whether there was an alternative prey. The number of alternate prey consumed also significantly differed between predators ( $P < 0.001$ ) with backswimmers being the most effective predator. Relatively few studies have tested for egg raft predation/destruction. Hence it is crucial that we conduct similar trials in other landscapes since such predators can prove to be key agents for the biological control of mosquitoes.

**Keywords** Prey choice · Oviposition · Biological control · Vector management · *Notonecta maculata* · *Sympetrum fonscolombii* · *Ommatotriton vittatus*

## Introduction

Egg predation can have long-term consequences for fitness and population dynamics, and its effects have been well studied in conservation biology, particularly for birds (e.g. Hansen & Errikstad, 2013) and reptiles (e.g. Leighton et al., 2009). Predation on eggs can also contribute significantly to controlling disease vectors and invasive species. Ecological approaches to controlling mosquitoes have focused largely on larval predation (e.g., see Lacy & Orr, 1994 for review). Far less explored is predation on mosquito eggs or egg rafts.

In mosquito genera, which lay eggs as a clutch (e.g., *Culex*, *Uranotaenia*, *Coquillettidia*, *Orthopodomyia*,

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and *Culiseta* species), a single clutch/egg raft can hold several hundred eggs. Since a single predation event can engulf all eggs in an egg raft, predators that feed on them have strong effects on mosquito abundance. In addition, unlike mosquito larvae, egg rafts are behaviorally unresponsive (i.e. have no antipredator behavior), thus predators who are also effective egg raft predators will be more effective in mosquito control. Hence, egg raft predation ecology may play a key role in mosquito biocontrol options (Blaustein et al., 2014; Segev et al., 2017), and studies are needed to identify such predators in different ecosystems.

There are relatively few studies on egg or egg raft predation in mosquitoes. Fire ants feed on individual eggs of some mosquito species that lay eggs in damp soil (Lee et al., 1994; Duhrkopfl et al., 2011). Once flooded, tadpoles may also consume the eggs (Bowatte et al., 2013). In mosquito-breeding sites, in addition to tadpoles several species of fish (Pramanik & Raut, 2008; Segev et al., 2017), salamanders (Blaustein et al., 2014) and insect predators (Chesson, 1984; Stav et al., 1999) also feed on the eggs and egg rafts, or destroy them. Breaking up or destroying of an egg raft, which causes the eggs to sink, can kill the mosquito embryo inside if disrupted early during egg development (Chesson, 1984; Mukherjee, personal observation).

Studies evaluating egg raft predation rates by different predators in the presence and absence of alternative prey are lacking. *Culiseta longiareolata* (Macquart, 1838) has been shown to avoid predation by *Notonecta* species when selecting oviposition sites, detecting the predator through predator-released kairomones (Blaustein et al., 2004; Silberbush et al., 2010). The larvae and pupae of this mosquito species are highly vulnerable to backswimmers (e.g. Blaustein et al., 1995; Blaustein, 1998; Stav et al., 1999) and newts and dragonflies (Mukherjee, unpublished data). We hypothesized that alternative prey presence should reduce predation on mosquitoes (e.g., Chesson, 1989; Blaustein, 1990), including on egg rafts. We tested our hypothesis by comparing egg raft predation (consumption)/destruction (disintegration and or sinking of an egg) of *C. longiareolata*, by three different aquatic predators in simulated temporary pools. We also tested if the presence of alternative prey, *Culex* mosquito larvae, influenced egg raft predation.

It is vital to study egg raft predation/destruction also in the context of understanding oviposition

habitat selection of mosquitoes. Numerous studies have shown that mosquitoes select patches for oviposition based on the predator and competitor composition in the habitat (see Vonesh & Blaustein, 2010 meta-analysis for review). The inferences drawn in such studies are often based on the number of egg rafts found in a given habitat, with lower numbers indicating a poor preference of risky or high-competition habitat. However, if egg raft predation by aquatic predators is indeed common, a low number of egg rafts could be a result of high egg raft predation, hence not an indicator of avoidance of the risky habitat by mosquitoes.

## Methods

The experiments were conducted in outdoor mesocosms—red plastic tubs (45 cm long × 55 cm wide × 20 cm deep) with 30 l of aged tap water at the Haifa University campus (~ 460 m above sea level, +32°45′35.17″, +35°1′17.32″) on June 2015. We used three mosquito larval predators: backswimmer adults (*Notonecta maculata*, Fabricius, 1794)—an actively foraging predator, dragonfly larvae [*Symptetrum fonscolombii*, (Sélys-Longchamps, 1776), late-instar larvae: ~ 20 mm body length]—a sit-and-wait predator and striped newt larvae [*Ommatotriton vittatus* (Gray, 1835); median snout-vent length = 37.1 mm; median weight = 0.27 g]—also a bottom-dwelling sit-and-wait predator, which sits in the vegetation. Our focal mosquito species used in this experiment was *C. longiareolata*, which is one of the most abundant species of mosquito in the study area.

## Study design

For each predator species, we tested how egg raft predation was affected by: (1) Absence of alternative prey—a tub with a single predator species (two individuals) and two (< 12 h old) *C. longiareolata* egg rafts; and (2) Presence of alternative prey—a tub with a single predator species (two individuals), two (< 12 h old) *C. longiareolata* egg rafts and 100 *Culex* (3rd–4th instar) larvae. *Culex* larvae were collected from cattle tanks located within a zoo on the Carmel mountains in Haifa, Israel.

In treatments with no alternative prey, the predators were added 15 min before the egg rafts. In treatments

with alternative prey, we first added the alternative prey followed by the predator (after 30 min) and then the egg rafts (after an additional 15 min). Every morning for 7 days, *C. longiareolata* egg rafts freshly laid from the previous night were added to the tubs which were covered with a fine mesh (to prevent additional mosquito oviposition). We checked for both egg raft and *Culex laticinctus* (Edwards, 1913) larvae predation the following morning (after 24 h). In total, we had six replicates for treatments with alternative prey and seven for treatments without alternative prey.

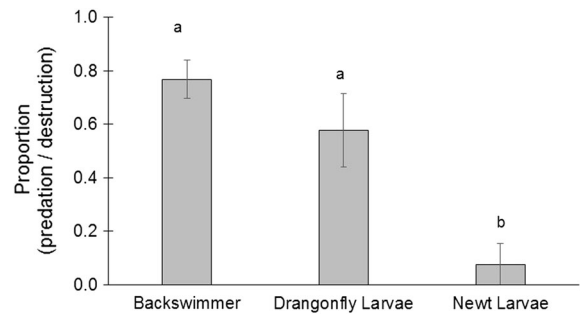
To rule out the possibility that the alternate prey were destroying or preying upon *C. longiareolata* egg raft, we also ran trials where we had two egg rafts along with 100 alternate prey in the water, but no predator. We did not find any evidence of *Culex* larvae predation on egg rafts.

## Data Analysis

We tested all data for normality using the Shapiro–Wilks test, and for equality of variance using Levene’s test. Since assumptions of normality were not met, to test how predator type and alternative prey affected egg raft predation; we used the Scheirer–Ray–Hare extension of the Kruskal–Wallis test (a nonparametric equivalent of the two-way analysis of variance, ANOVA) followed by a Dunn’s post hoc test (Sokal & Rohlf, 1995). We also tested for differences in the proportion *Culex laticinctus* larvae consumed by the different predators using a one-way ANOVA followed by a Tukey’s HSD posthoc test. For this, we first calculated the proportion of prey consumed followed by an arcsin-square root transformation. All analyses were conducted in R (Version 3.5.0)

## Results

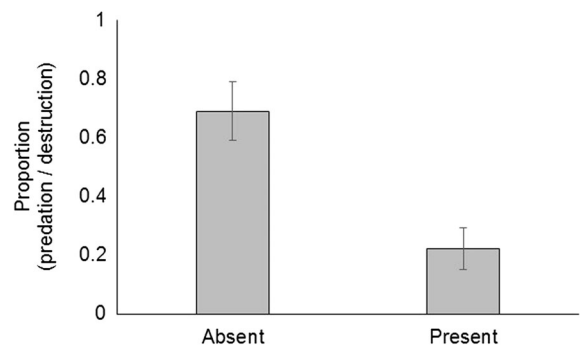
The number of egg rafts eaten/destroyed were significantly affected by the type of predators (Scheirer–Ray–Hare test,  $df = 2$ ,  $SS = 1800$ ,  $H = 16.19$ ,  $P < 0.001$ ; Fig. 1). On an average, while backswimmers destroyed 77% of the egg rafts, dragonfly larvae and newts ate 58% and 8% of the egg rafts respectively. Dunn’s post hoc test (Kruskal–Wallis multiple comparisons with  $P$  values adjusted with the Benjamini–Hochberg method) indicated no difference in egg rafts eaten/destroyed between backswimmers and



**Fig. 1** Differences in *Culiseta longiareolata* egg raft predation/destruction by three aquatic predators. All trials started with two egg rafts, so the proportion predation or destroyed is mean/2. Error bars indicate mean (proportion)  $\pm$  standard error. Different letters above the bars represent statistically significant differences ( $P < 0.05$ , Dunn’s post hoc test post hoc analysis) between treatments

dragonfly larvae ( $P = 0.26$ ; effect size—Cohen’s  $d = 0.49$ , effect-size  $r = 0.24$ ). However there was a significant difference between backswimmers and newts ( $P < 0.001$ ; effect size—Cohen’s  $d = 2.58$ , effect-size  $r = 0.79$ ) and dragonflies–newts ( $P = 0.01$ ; effect size—Cohen’s  $d = 1.25$ , effect-size  $r = 0.53$ ). The newts were the least effective egg raft predators.

The presence of alternate prey significantly affected egg raft predation (Scheirer–Ray–Hare test,  $df = 1$ ,  $SS = 1094.98$ ,  $H = 9.85$ ,  $P < 0.01$ ; effect size—Cohen’s  $d = 1.20$ , effect-size  $r = 0.51$ ; Fig. 2). Sixty-nine percent of egg rafts were preyed upon/destroyed in the absence of alternate prey compared to 11% when alternate prey was present.



**Fig. 2** Difference in egg raft predation/destruction in the presence or absence of alternate prey (3rd–4th instar *Culex* larvae). All trials started with two egg rafts, so the proportion predation or destroyed is mean/2. Error bars indicate mean  $\pm$  standard error. Data aggregates across all predator treatments

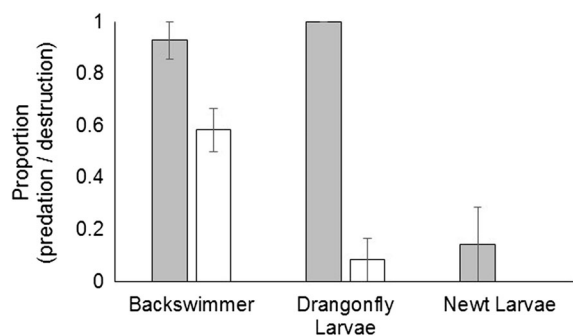


There was no significant interaction between predator-type and alternate-prey presence (Scheirer–Ray–Hare test,  $df = 2$ ,  $SS = 551.44$ ,  $H = 4.96$ ,  $P = 0.08$ ; Fig. 3). However, while backswimmers reduced egg raft destruction by 35% in the presence of alternate prey (effect size—Cohen's  $d = 1.75$ , effect-size  $r = 0.66$ ), dragonfly larvae showed a 92% reduction in egg raft predation (effect size—Cohen's  $d = 6.35$ , effect-size  $r = 0.95$ ). As expected, no egg rafts were eaten/destroyed in the two control treatments (see methods).

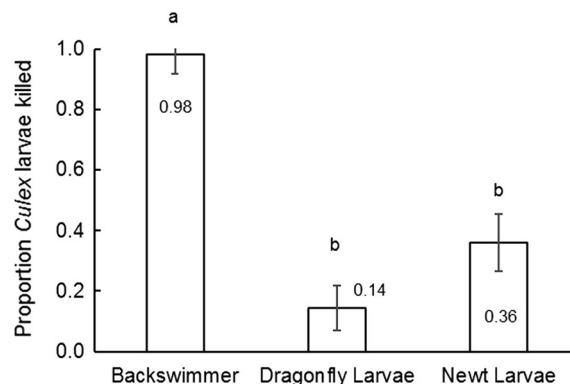
The number of *Culex laticinctus* larvae killed significantly varied between the three predator types (ANOVA— $F_{2,15} = 47.88$ ,  $P < 0.001$ ; Fig. 4). The backswimmers were the most effective larval predator consuming 98% of *Culex* larvae. They killed a significantly higher number of mosquito larvae compared to newts (Tukey post hoc test:  $P < 0.001$ ; effect size—Cohen's  $d = 4.00$ , effect-size  $r = 0.89$ ) and dragonflies (Tukey post hoc test:  $P < 0.001$ ; effect size—Cohen's  $d = 6.05$ , effect-size  $r = 0.95$ ). However, newts and dragonflies did not differ in larval predation (Tukey post hoc test:  $P = 0.09$ ; effect size—Cohen's  $d = 1.22$ , effect-size  $r = 0.52$ ).

## Discussion

Controlling mosquito populations is a major priority in applied ecology and epidemiology. Although previous studies have focussed on mosquito larval predation (e.g., see Lacy & Orr, 1994 for review) and recently on oviposition habitat selection in response to risk of



**Fig. 3** Differences in egg raft predation among the three mosquito predators, in the presence (empty bar) or absence (filled bar) of alternate prey. All trials started with two egg rafts, so the proportion predation or destroyed is mean/2. Error bars indicate mean  $\pm$  standard error



**Fig. 4** Differences in the proportion 3rd–4th instar *Culex* larvae preyed upon (mean number alive/100) by the different predators over 24 h. Numbers next to the bar indicate mean (back-transformed) proportion *Culex* consumed per day (out of 100 larvae added) by the predators. The analysis was carried out on *Arcsine Square root* transformed proportion data. Error bars indicate back-transformed mean  $\pm$  standard error. Letters above the bars represent statistically significant differences ( $P < 0.05$ , Tukey's HSD post hoc analysis)

predation (Vonesh & Blaustein, 2010), our experiment clearly shows that the three predators posed different levels of risk to the egg rafts. While there was only a single instance of predation by newts (in the absence of alternative prey), generally they did not pose any risk to the egg rafts, although they did feed on mosquito larvae. This is in contrast to a study of the Near Eastern fire salamander [*Salamandra infraimaculata*, (Martens, 1885)] in the same region, where egg raft survival was reduced by up to 50% by premetamorphosing fire salamanders (Blaustein et al., 2014).

Backswimmers destroyed all the egg rafts and hence proved to be the most effective among the three predators. We provide a visual example of egg raft destruction by backswimmers on the following link: <https://www.youtube.com/watch?v=lazxuvFgGs> On a number of occasions, after backswimmers attacked and disintegrated an egg raft, a large fragment of the egg raft remained. The backswimmer attacked it again, causing all the eggs to sink. Similar to what was observed by Chesson [1984; for *Notonecta hoffmani* (Hungerford, 1925) and *N. kirbyi* (Hungerford, 1925)], the backswimmers in our experiment did not prey upon (i.e., did not hold on to an egg for long), but destroyed all the egg rafts. This caused the individual eggs to separate off from egg raft and sink.

It is not clear what the ecological benefits of egg destruction are for backswimmers. Unlike dragonflies

and newts, backswimmers prey heavily on neuston, including insects that become trapped at the water surface. However *Notonecta* are known to feed on large zooplanktons (Scott & Murdoch, 1983; Murdoch & Scott, 1984). Since we did not observe the submerged mosquito eggs under a microscope, we are not sure if backswimmers managed to pierce into the eggs. In nature, the destructive behavior of backswimmers could either be merely incidental or it helps interfere with the feeding habits of other competing (mosquito) larval and egg raft predators.

Notonectids frequently grab onto structural elements (e.g. plants, sticks, etc.) and hold on to them. Since there were no structural elements in our tubs apart from the floating egg rafts, backswimmers may have destroyed rafts by simply clinging on to them. If this is true, then our observed rate of destruction may be ecologically unrealistic as in natural ponds they would have lots of other structural elements to hold onto. Future research should test if the presence of floating structural elements reduces egg raft destruction.

*Culiseta longiareolata* avoids *Notonecta maculata*-conditioned water where *Notonecta* themselves are not present to consume egg rafts (Blaustein et al., 2004; Silberbush et al., 2010), and this is true for *Anisops*-conditioned water (*Anisops* is also a Notonectidae) (Eitam et al., 2002) and caged *Notonecta* as well (Blaustein and Mangel, unpublished data). In Missouri, Blaustein et al. (2005) have also found *Culex* species to oviposit far fewer egg rafts in pools with *Notonecta irrorata* (Uhler, 1879) conditioned water. We have now found in this current work that the low proportion of egg rafts deposited in Notonectidae pools do get destroyed by notonectids. This was also found by Chesson (1984) in California. Caged dragonfly nymphs, *Anax imperator* [(Leach, 1815); Stav et al., 1999, 2000] and caged *Sympetrum fonscolombii* (Eitam et al. unpublished data) and caged *Salamandra infraimmaculata* larvae (Blaustein et al., 2014) also did not affect *C. longiareolata* oviposition. And in the case of these two species of dragonfly larvae and *Salamandra* larvae, some egg rafts in the presence of dragonfly larvae and many egg rafts deposited in the presence of *Salamandra* do get consumed. Hence, although predator kairomones of some predators are an important deterrence for some mosquito species, few do lay eggs in the presence of predators.

When we look at the interaction between dragonfly larvae of *Sympetrum fonscolombii* and mosquitoes, we found that the presence of an alternative prey significantly affected egg raft predation by these dragonflies. While they always preyed upon egg rafts when no larvae were present (except one instance when it fed on one egg raft), there was no egg raft predation by these dragonflies when *Culex laticinctus* larvae were present (Fig. 3). This is in contrast to the behavior of another dragonfly species, *Anax imperator*. Stav et al. (1999) found that in 14.3% of cases egg rafts disappeared when they placed a *C. longiareolata* egg raft with an *A. imperator* larva in a 1L tub (compared to 30L containers we used). Given the larger container size in this study, our results suggests that *S. fonscolombii* is a more effective egg raft predator than *A. imperator*. While experimental conditions of the two studies may not be exactly similar, but future studies should look at the differences in the foraging behavior of these two dragonflies. It is likely that *Sympetrum fonscolombii* maybe a more active predator compared to *A. imperator*.

Knowledge about egg raft predation and/or destruction can complement studies who aim to understand the oviposition decisions of animals in the context of perceived risk of predation. For example, oviposition studies are interested in understanding whether female mosquitoes choose a certain patch based on the quality of the habitat (quality based on food availability, or presence of competitors and predators; see Vonesh & Blaustein, 2010). If our knowledge about egg raft predation is incomplete, such oviposition studies will make incorrect inferences. For instance, fewer egg rafts in a patch will be mistakenly attributed to oviposition habitat selection (Blaustein et al., 2014). However, fewer egg rafts may simply be a result of a high incidence of egg raft predation. We find evidence for this not only in our current study, but it has also been shown by Chesson (1984) for two backswimmer species and by others (see Blaustein et al., 2004; Silberbush et al., 2010). Hence, fewer egg rafts may be explained by both egg raft disruption or predation and oviposition habitat selection in response to the risk of predation.

Biological control of pests and vectors is now widely accepted and practised throughout the world, considering minimum adverse effects on non-target organisms and preservation of the faunal biodiversity. Since mosquitoes are the main insect vectors for

several diseases (e.g. malaria, dengue, chikungunya, zika, etc.), studying mosquito egg raft predation/destruction is important for human health. This should involve a systematic experimental approach to study the effectiveness of local aquatic predators as larval and egg raft predation.

To increase realism perhaps future work should assess how combinations of aquatic predators that often co-occur in nature affect egg raft survival. The complexity of the aquatic food web has been shown to have impacts on the survival and emergence of aquatic insects (i.e. Pope et al., 2009; Rudman et al., 2016). Perhaps future feeding experiments could continue long enough to track the fate of these eggs to larvae as well. If native aquatic predators are as effective as the backswimmers in egg raft predation, they can play an essential role in biological control of mosquitoes. While it is true that raft destruction could be an important force in limiting the abundance of adult mosquitos (which ultimately is what matters in disease vector control), it is not necessarily clear how much this will matter because it will depend on mortality rates from other factors in the egg and larval stages. An experiment which allows for larval predation but not egg (or egg raft) predation would be beneficial.

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