# Co-occurring *Notonecta* (Hemiptera: Heteroptera: Notonectidae) species differ in their behavioral response to cues of *Belostoma* (Hemiptera: Heteroptera: Belostomatidae) predation risk

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## Abstract

Predators affect prey through direct consumption as well as by inducing prey to defensively alter their phenotypes, including behavioral phenotypes, to maximize survival under predation risk. Closely related sympatric prey species with shared natural enemies may resolve behavioral trade-offs under predation risk differently. In a laboratory experiment, we investigated two co-occurring semi-aquatic backswimmer congeners (Heteroptera: Notonectidae), which exhibit differences in their degree of habitat specialization across a gradient of habitat permanence. *Notonecta irrorata* primarily occur in ephemeral ponds, whereas *N. undulata* are habitat generalists that are commonly found in both permanent and ephemeral ponds. We tested whether the two species differed in antipredator responses to both visual and chemical cues of a shared predator, the giant water bug (Heteroptera: Belostomatidae), in a fully factorial design. The generalist species, *N. undulata*, exhibited reductions in activity in the presence of predator chemical cues only, whereas the specialist species, *N. irrorata*, remained consistently active across predator cue treatments. Our work shows that there are species-specific differences in how prey assess or respond to predation risk. The varying propensities of these backswimmer congeners to behaviorally respond to a shared predator, and differences in their behavior when exposed to different predation risk cues may be linked to underlying divergence in their life-history strategies.

**Keywords:** phenotypic plasticity, antipredator behavior, predation risk, backswimmers, *Notonecta*

## Introduction

While the consumptive effects of predators on prey result in mortality, the mere presence of a predator can trigger suites of behavioral, morphological, and physiological responses in prey ("non-consumptive effects"; reviewed in Lima 1998). The costs that predators impose on prey performance via non-consumptive effects have been increasingly appreciated in studies of predator-prey interactions (Chivers and Smith 1998, Hoverman et al. 2005). Beyond individual fitness effects, non-consumptive effects are of ecological importance because they can influence prey population dynamics and community structure (McPeek 1990, McPeek 1998, Preisser et al. 2005, Preisser and Bolnick 2008).

Many empirical studies indicate that prey generally reduce their activity and/or seek refuge when threatened by predators in order to minimize encounters (Lima and Dill 1990, Skelly and Werner 1990, Skelly 1994, McPeek 1996, Anholt and Werner 1998, Gyssels and Stoks 2006, Ferrari et al. 2010). However, antipredator responses are not universal; not all prey will plastically respond to predation risk or respond in the same way (Skelly 1994, Relyea 2001, Boersma et al. 2008). Some prey increase activity by moving away in response to high predation risk (Miyasaka and Nakano 2001, Walker et al. 2005). For instance, some fish will escape predation by rapidly accelerating away from the predator, and increased swimming performance is often associated with decreased mortality from predation (Walker et al. 2005). Other prey do not alter activity levels (e.g. *Ischnura* damselflies: McPeek 1996, tadpoles of desert ephemeral ponds: Woodward 1983), potentially decreasing the non-consumptive effects predators impose, but at the cost of increased predation risk.

Prey behavioral responses depend on effectively detecting predators (Sih 1987, Lima and Dill 1990); prey must use reliable cues of predation risk (Koops 2004). Olfactory cues often provide critical information about the environment encountered, particularly in aquatic systems in which predator detection often involves using signature kairomones of the predator and chemical alarm cues of consumed conspecifics in order to assess risk and respond accordingly (Petranka et al. 1987, Kats and Dill 1998, Fraker 2008, Fraker et al. 2009, Schoeppner and Relyea 2009, Ferrari et al. 2010, Costa and Vonesh 2013). However, in some aquatic organisms, visual cues are important in detecting predation and initiating the antipredator response (Becker and Gabor 2012, Hettyey et al. 2012). Therefore, the relative importance and magnitude of predation risk may be cue-dependent and species-specific. One way to investigate the diversity of defensive behavioral mechanisms is to examine the defenses of closely related, sympatric prey species which share common predators.

*Notonecta* backswimmers (Heteroptera: Notonectidae), a guild of aquatic insects which inhabit freshwater ponds, provide a useful system to examine how congeners respond to cues of perceived predation risk. *Notonecta* species have been shown to be ecologically similar (Gittleman 1973), competing through usage of overlapping resources (Streams 1987a, 1987b, Hungerford 1919). The two species we studied, *Notonecta undulata* Say and *Notonecta irrorata* Uhler, differ in their habitat breadth across ponds. *Notonecta irrorata* tend to be specialists of fishless, ephemeral ponds, whereas *N. undulata* are habitat generalists that are commonly found in ephemeral ponds, but can also occupy permanent ponds with fish (Cook and Streams 1984). Previous studies examining behavioral responses of *Notonecta* to predator cues focused on understanding predator-induced dispersal (McCauley and Rowe 2010, Baines et al. 2014). However, little is known about whether predators induce changes in activity or other behaviors in *Notonecta*. To our knowledge, no studies have compared antipredator responses across species in the backswimmer guild, with the exception of a study of fish predators, which found that backswimmer species which occur in fishless ponds tend to be more vulnerable to fish predation, suggesting that predation is an important determinant of backswimmer assemblage patterns (Cook and Streams 1984). The species-specific responses of backswimmers to the threat of invertebrate predation are unknown, and this system provides an opportunity to understand if and how variation in antipredator behavioral responses is linked to differences in habitat breadth and underlying life-history trade-offs in sympatric prey species.

Here, we present results from an experiment in which we evaluated differences in antipredator behavior of two co-occurring congeners, *N. undulata* and *N. irrorata* in response to an invertebrate predator, *Belostoma flumineum* Say (Heteroptera: Belostomatidae). We assessed behaviors of single *Notonecta* adults in the presence and absence of predator chemical and visual cues to address the following questions: (1) Do *Notonecta* congeners exhibit predator-induced behavioral plasticity in activity? (2) Do habitat generalists (e.g. *N. undulata*), and habitat specialists (e.g. *N. irrorata*) respond differently to cues of a shared predator? (3) How do visual and chemical cues of perceived predation risk influence defensive changes in prey activity in these two species? We expected that both species would respond to predators by reducing activity but that the magnitude of activity change would differ if these species resolve the trade-offs associated with predator avoidance differently. According to the adaptive plasticity hypothesis, if adaptive plasticity evolves under selection caused by variable environments, then organisms that inhabit more variable environments (for instance, encountering a diverse set of predators) across the heterogeneous landscape should exhibit phenotypes that are more plastic (Klopfer and MacArthur 1960, Via and Lande 1985, Moran 1992, van Tienderen 1997, Relyea 2001, Van Buskirk 2002). Specifically, habitat generalists such as *N. undulata*, may have a higher degree of flexibility in behavior to a wide variety of environmental contexts, such as predation risk. Whereas, *N. irrorata*, which is a habitat specialist, may exhibit a narrower range of behavioral traits. We also predicted that chemical cues may be more important in this antipredator response than visual cues, regardless of *Notonecta* prey species, because many sit-and-wait predators (such as *B. flumineum*) are adapted to minimize visual detection by prey.

## Methods

### ***Study organisms***

All experiments were conducted at the Koffler Scientific Reserve (KSR; 44° 01' N, 79° 32' W) in King City, Ontario, Canada. We examined behavioral plasticity in two backswimmer species in the genus *Notonecta, N. undulata* and *N. irrorata,* in response to a heteropteran predator, *Belostoma flumineum*. These *Notonecta* species co-occur in fishless pond communities (Streams 1992) where belostomatids are common invertebrate top predators. These backswimmer species have a high degree of dietary overlap, but within a given pond *N. undulata* tends to occur in a variety of microhabitats, whereas *Notonecta irrorata* is more specialized to shady habitats (Hungerford 1919, Hungerford 1933, Streams and Newfield 1972, IMCF, pers. obs.). In the fishless ponds where these two *Notonecta* species co-occur, they frequently encounter the predator, *Belostoma flumineum*. Belostomatids are generalist sit-and-wait predators and are top invertebrate predators in many freshwater systems (Menke 1979, Tobler et al. 2007, Boersma et al. 2014). Belostomatids are opportunistic hunters and ambush predators which camouflage quite well against the benthos and which forage across the day and night (Schumann et al. 2012); thus, their prey may use visual or chemical cues to detect the presence of the predator.

### ***Collection***

We collected 53 adult *Notonecta undulata* from a fishless pond at KSR on May 9, 2016 and held them in two mesh-covered stock buckets. We collected belostomatid predators from the same pond on May 10, 2016. Thirteen belostomatid predators were held together in a bucket of pond water which would later be used as predator chemical cue water. Fifty *N. irrorata* from the same pond were collected on July 19-20, 2016 and housed in the same way as *N. undulata*. Differences in collection times between these two species result from differences in their phenology and correspond with the peak times of abundance of adults. For the *N. irrorata* trials, ten new *Belostoma* were collected from the same site and held in the same conditions as the earlier trials with *N. undulata*. *Notonecta* were fed mosquito larvae and plankton *ad libitum*, thus avoiding hunger-induced elevation in activity levels during the trials. *Notonecta* were also fed to the predators prior to the start of the trials, a method commonly used in non-lethal predator studies in order to release conspecific alarm cues into the predator water (Abjornsson et al. 2000, Paterson et al. 2013, Baines et al. 2014).

### ***Experimental setup***

Glass aquaria (40 x 20 x 25 cm high) were filled with pond water from the collection source. Pond water was used because other studies have reported that some water types, such as dechlorinated tap water, may alter the natural degradation processes of predator cues (Ferrari et al. 2007, Paterson et al. 2013). We added approximately 5 g of dried reeds (*Phragmites*) to each aquarium to simulate natural pond conditions.

We placed a predator chamber in the center of each aquarium which consisted of a 355-ml clear plastic lockable container weighted down by ~75 g of rocks. There were four predator cue treatments: a) visual and chemical cues: a single belostomatid was enclosed inside the predator chamber that had been perforated with holes, and the chamber was filled with water from the predator stock tank, b) visual cues only: a single belostomatid was enclosed inside an unperforated predator chamber and further sealed using duct tape around the lid, c) chemical cues only: the empty perforated chamber was filled with water from the predator stock tank, and d) no predator cues: an empty chamber was present but no predator cues were added (Fig. 1a-d). Each treatment was replicated 10-11 times for *N. undulata* and 11-12 times for *N. irrorata*. *Notonecta* experimental units were randomly assigned to treatments with trials conducted in randomized order.

Aquaria for behavioral trials were prepared and lined up on a shelving unit indoors with ample natural lighting in order to be videotaped using three high-definition cameras (SJCAM SJ4000 Wi-Fi 1080p HD Action Camera Sport DVR). The sides of the tanks were covered with waterproof paper in order to avoid disturbances or behavioral responses to backswimmers or *Belostoma* caged in adjacent aquaria. Backswimmers were randomly assigned to treatments and *Belostoma* to be placed in the "Visual+Chemical" and "Visual" treatments were randomly selected.

### *Measures of* **Notonecta** *activity*

For each observational trial, a single notonectid was collected from the stock bucket and placed inside each aquarium where activity measures were recorded for 15 minutes following an initial habituation period of 3 minutes. Backswimmers were video-taped for the duration of the trials and videos were played back in order to measure activity precisely. During playback, we recorded the start and end times of swimming activity during each trial. It was not possible for the observer to be blind to treatment because of the nature of the predator cue treatments (Fig. 1a-d). Swimming activity was quantified as the total time spent swimming in the trial. Following the activity observation period, backswimmers were exposed to a startle stimulus which consisted of a slap on the surface of the water with a plastic fly swatter, to examine behavioral plasticity to a simulated predation attack. The startle response time was recorded as the time it took for each individual to stop swimming following the startle stimulus.

### *Statistical analyses*

To assess whether the type of predator cue influenced *Notonecta* activity, we conducted two separate 2x2 ANOVAs for the two response variables: total time spent swimming and startle response time. In both cases, the predictors were the presence and absence of visual and chemical cues, and the interaction between visual and chemical cues. Both total swim time and startle response time were log+1 transformed before analyses in order to normalize their distributions. These analyses were conducted separately for each species because experimental trials were not randomized by species, since the two species were collected at different times. All statistical analyses were performed in R version 3.2.3 (R Core Team, 2015).

## Results

*Notonecta undulata* exhibited behavioral plasticity in response to predation risk. *Notonecta undulata* reduced swimming activity in the presence of the predator, but only when they were exposed to chemical cues (Chemical: $F_{1,38} = 13.00$, $p = 0.0009$; Fig. 2a). Visual cues did not influence swimming activity (Visual: $F_{1,38} = 0.33$, $p = 0.57$) nor did visual cues modify the effect of chemical cues on swimming activity (Visual × Chemical: $F_{1,38} = 0.12$, $p = 0.73$). Similarly, *N. undulata* swam for shorter periods of time following the startle stimulus when exposed to chemical cues of the predator (Chemical: $F_{1,38} = 7.56$, $p = 0.009$; Fig. 3a). Visual cues did not influence the behavioral response to the startle stimulus (Visual: $F_{1,38} = 0.61$, $p = 0.44$) and did not interact with chemical predator cues (Visual × Chemical: $F_{1,38} = 0.012$, $p = 0.92$).

Across all predator treatments, *N. irrorata* was much more active than *N. undulata* (average swim times of 112.7 s and 64.3 s, respectively). *Notonecta irrorata* did not exhibit behavioral plasticity in response to the non-lethal predator; there was no effect of the presence of the different predator cues on *N. irrorata* swimming activity (Visual: $F_{1,42} = 2.91$, $p = 0.095$; Chemical: $F_{1,42} = 0.0001$, $p = 0.99$; Visual × Chemical: $F_{1,42} = 0.05$, $p = 0.82$; Fig. 2b). Additionally, *N. irrorata* did not change their startle response time when exposed to the different types of predator cues (Visual: $F_{1,42} = 1.80$, $p = 0.19$, Chemical: $F_{1,42} = 0.09$, $p = 0.76$, Visual × Chemical: $F_{1,42} = 1.20$, $p = 0.28$; Fig. 3b).

## Discussion

### ***Behavioral plasticity in activity among co-occurring congeners***

In this study, we focused on one aspect of behavioral plasticity in response to a non-consumptive aquatic invertebrate predator: activity level. In the backswimmers we studied, the habitat generalist, *N. undulata*, plastically responded to chemical cues of the predator by reducing activity, whereas the habitat specialist, *N. irrorata*, did not exhibit behavioral plasticity but were consistently active. To our knowledge, this is the first study that tests how the behavior of closely-related, sympatric backswimmers depends on both visual and chemical cues of the presence of a shared predator.

Why might two closely related congeners not respond in the same way to a predator they both commonly experience? According to theory, the adaptive plasticity hypothesis proposes that species which encounter variable environments should exhibit high phenotypic plasticity (Via and Lande 1985, Relyea 2001, Relyea 2004). We speculate that the higher flexibility in behavior in response to changing predation risk (termed anti-predator decision making; Lima 1998), in *N. undulata*, may be attributed to the fact that they are habitat generalists, which persist across many environments that differ in the identity of the top predator. *Notonecta undulata* may face a disproportionate risk of predation and may benefit from being able to respond flexibly to a variety of environmental conditions encountered. For habitat specialists, like *N. irrorata*, however, the costs of behavioral plasticity in activity may outweigh the benefits and they may perform better by consistently exhibiting the same behavioral phenotype (i.e., being consistently active). This species may be limited disproportionately by other factors such as resource acquisition since they are characteristically very active and larger-bodied than *N. undulata*, and likely have high metabolic demands. Thus, if *N. irrorata*'s riskier behavior also coincides with a higher rate of energy intake, then we would expect this species to accept a greater risk of predation. These results provide some support for the pace-of-life syndrome hypothesis which proposes that closely related species should differ in covarying suites of physiological (e.g. metabolic), life history, and behavioral traits in order to successfully persist in the same ecological environment (Ricklefs and Wikelski 2002, Reale et al. 2010).

Empirical work in other prey assemblages provides evidence that the way in which prey differentially resolve activity-mediated life history trade-offs may be linked to habitat breadth and degree of habitat specialization. For example, McPeek (1990) compared antipredator behavior in *Ischnura* and *Enallagma* damselflies. *Ischnura spp.* tend to be habitat generalists, occurring in environments with and without fish, while *Enallagma spp.* tend to segregate across predator habitats and specialize in habitats with either fish or dragonfly top predators. *Ischnura* damselflies were more active than *Enallagma* damselflies, across a range of habitat types with different top predators, and had higher mortality from both fish and dragonfly predators than *Enallagma* (McPeek 1990). Therefore, there may be differences in the way specialists and generalists resolve life-history trade-offs as the generalist may be disproportionately at risk of predation (McPeek 1996). Across a gradient of predation risk, McCauley (2008) showed that in a guild of dragonfly larvae, generalist species which coexist with a diverse set of top predators vary in their activity levels, and the more often they occur with fish the less active they were. Similarly, in other co-occurring damselflies with different life histories, *Erythromma najas* and *Lestes sponsa*, Slos et al. (2009) found that these species use two fundamentally different behavioral strategies to cope with environmental challenges such as gradients in predation risk. The former, which typically occurs in environments with fish, have fixed low activity and the latter, which can co-occur with fish but prefer more temporary environments without fish exhibits consistently high activity and fast growth rate (Slos et al. 2009).

The threat-sensitivity hypothesis put forward by Sih (1986), proposes that prey adjust their activity based on the level of threat imposed by the predator. Therefore, antipredator responses depend largely on risk level (Chivers and Smith 1998, Milano et al. 2010). The two species we compared may differ in the risk they face from these predators. For instance, coloration, palatability, and swimming speed may play a role in prey vulnerabilities (Skelly 1994). In our system, the species that does not exhibit predator-induced behavioral change, *N. irrorata*, may have other morphological and behavioral traits that allow it to evade predation more successfully than *N. undulata*. For instance, *N. irrorata* is darker than *N. undulata*, likely making them more difficult to detect in ponds with high turbidity, common in more temporary ponds, or in the shady portions of ponds in which they are most commonly found. It is also the larger species and has higher swimming speeds coupled with generally higher activity levels than *N. undulata* (IMCF, pers. obs.). Being larger as well as consistently fast and active may allow them to escape predators even if attacked more often than *N. undulata*.

### ***Responses to visual and chemical predator cues***

Our results also demonstrate the importance of chemical cues in shaping the antipredator response for one of the prey species, *N. undulata***,** as this species is less active in the presence of predator chemical cues. Particularly in aquatic systems, these predator chemical signals may play an important role in shaping predator-prey dynamics as chemically-mediated, non-consumptive effects can potentially be strong even at low predator density. In fact, previous studies have noted that semiochemicals which transmit information within and between species are dominant in aquatic environments and may be critical in mounting an antipredator response for some species (Werner and Anholt 1993, Gyssels and Stoks 2006, Ferrari et al. 2010, Milano et al. 2010).

Interestingly, visual cues of the non-lethal predator did not stimulate behavioral plasticity in either co-occurring species of backswimmer (Fig. 2-3). Other studies examining the behavioral responses to predator signals in an aquatic setting have found that chemical signals may be more reliable than visual cues (Stauffer and Semlitsch 1993, Paterson et al. 2013). This may be because other factors in aquatic environments including water turbidity, low prey visual ability/visual field, and cryptic coloration of predators decrease the ability of animals to accurately visually detect predators. These factors may be especially important in this system with the belostomatid predator, as they are sit-and-wait ambush predators, camouflage quite well in the benthos, and spend time lower in the water column than the backswimmers which are usually swimming further up in the water column or clinging to vegetation near the surface (Menke 1979, IMCF, pers. obs.). These observations suggest that limitations in their visually-mediated predator detection may provide insight into why visual cues are not used for both species, and why chemical cues are more important in the detection and response to predation risk for *N. undulata*.

Our findings are similar to previous work showing that antipredator responses in two closely related tadpoles are strongest in the presence of chemical cues alone, regardless of cue combination (Stauffer and Semlitsch 1993). However, our results contrast with previous work supporting the interactive effects of cues on prey behavioral plasticity, indicating that all cues are important (Becker and Gabor 2012, Hettyey et al. 2012). For example, in *Rana temporaria* tadpoles, the greatest decline in activity in response to the predator occurred when all cues were present (Hettyey et al. 2012). Similarly, in the fountain darter (*Etheostoma fonticola*), the combination of visual and chemical cues was necessary for detecting predator presence and eliciting the strongest antipredator response (Becker and Gabor 2012).

In aquatic environments, it has been well-established that chemical cues are key primary signals through which prey assess and detect changes in the local environment; such as those relaying signatures of a predator's presence. Interestingly though, antipredator responses to predator cues are not universal and here we show that two co-occurring aquatic insects that differ in habitat breadth across the specialist/generalist divide, assess and respond to predation risk differently. The differential behavioral responses to predation risk observed here in two co-occurring backswimmer congeners potentially reflect differences in prey ecological performance (e.g. Skelly and Werner 1990), and degree of habitat specialization across the spatially discontinuous landscape (e.g. McPeek 1990, 1996) as predicted by the adaptive plasticity hypothesis (Via and Lande 1985, Moran 1992, van Tienderen 1997, Relyea 2001, Van Buskirk 2002). In aquatic habitats which lack fish, invertebrate predators such as the belostomatids studied here play a large role in structuring prey communities, and studies show that these invertebrate predators influence patterns of distribution in prey species both directly through consumption but also through the behavioral responses of prey (Crowley and Johnson 1982, Briers and Warren 1999). However, little is known about the proximal mechanisms underlying the diversity of threat-sensitive responses to predator cues (see Mitchell et al. 2017 for a recent review of the current state of our understanding and of the mechanistic gaps in this field). We can only speculate that the ways in which notonectids assess the costs and benefits of activity under predation risk may be closely and reciprocally linked with the degree of regional habitat specialization and shaped by their life-history trade-offs, and we argue that more work is needed to gain a better understanding of the detailed mechanisms underlying the role of non-consumptive predators on the divergence of co-occurring species behavioral phenotypes or divergence in life-history trade-offs. Use of the pace-of-life syndrome hypothesis framework (Ricklefs and Wikelski 2002, Reale et al. 2010) may aid our understanding of the role of life-history strategies and the potential costs and consequences of behavioral plasticity to predation risk maintaining interspecific variation in behavioral reaction norms.

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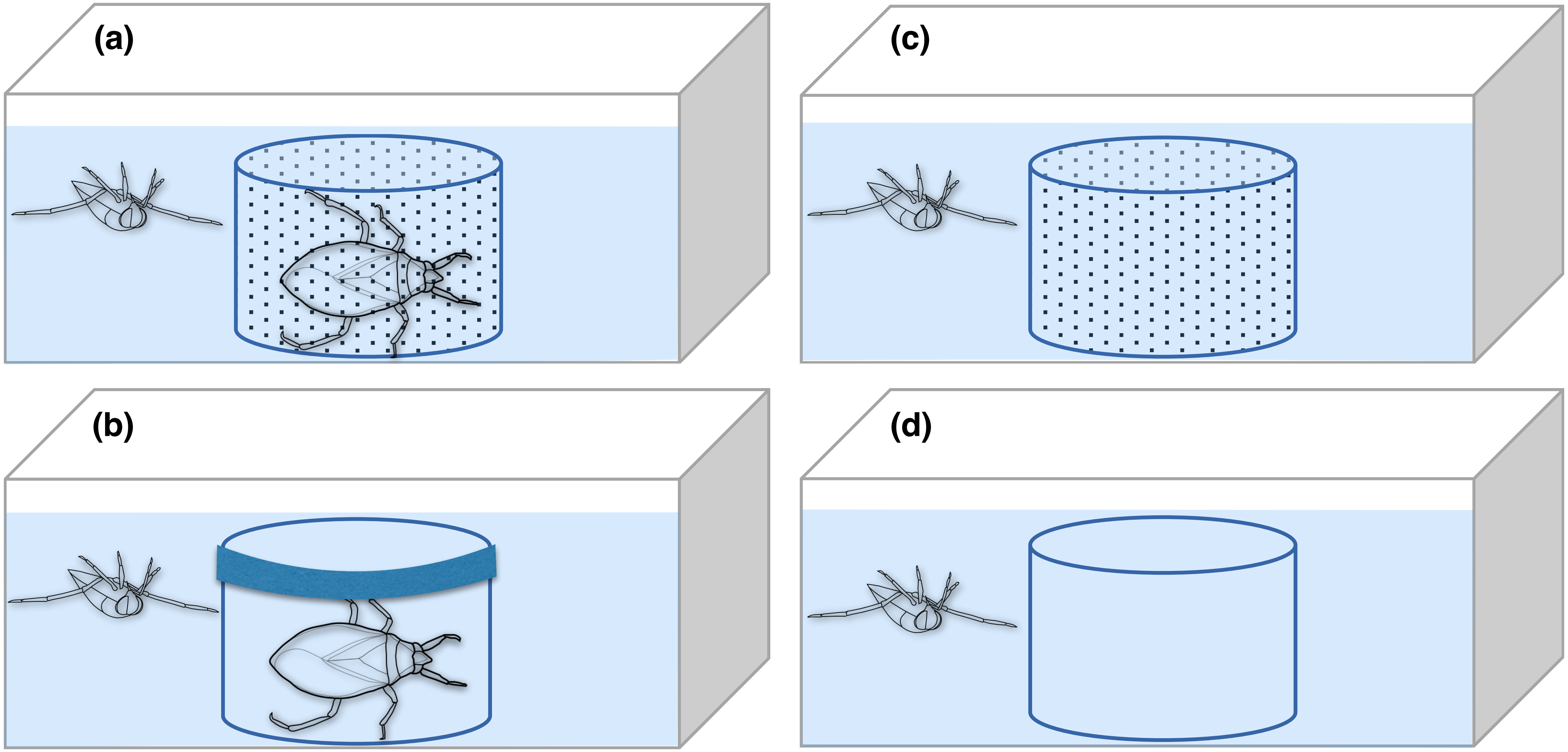
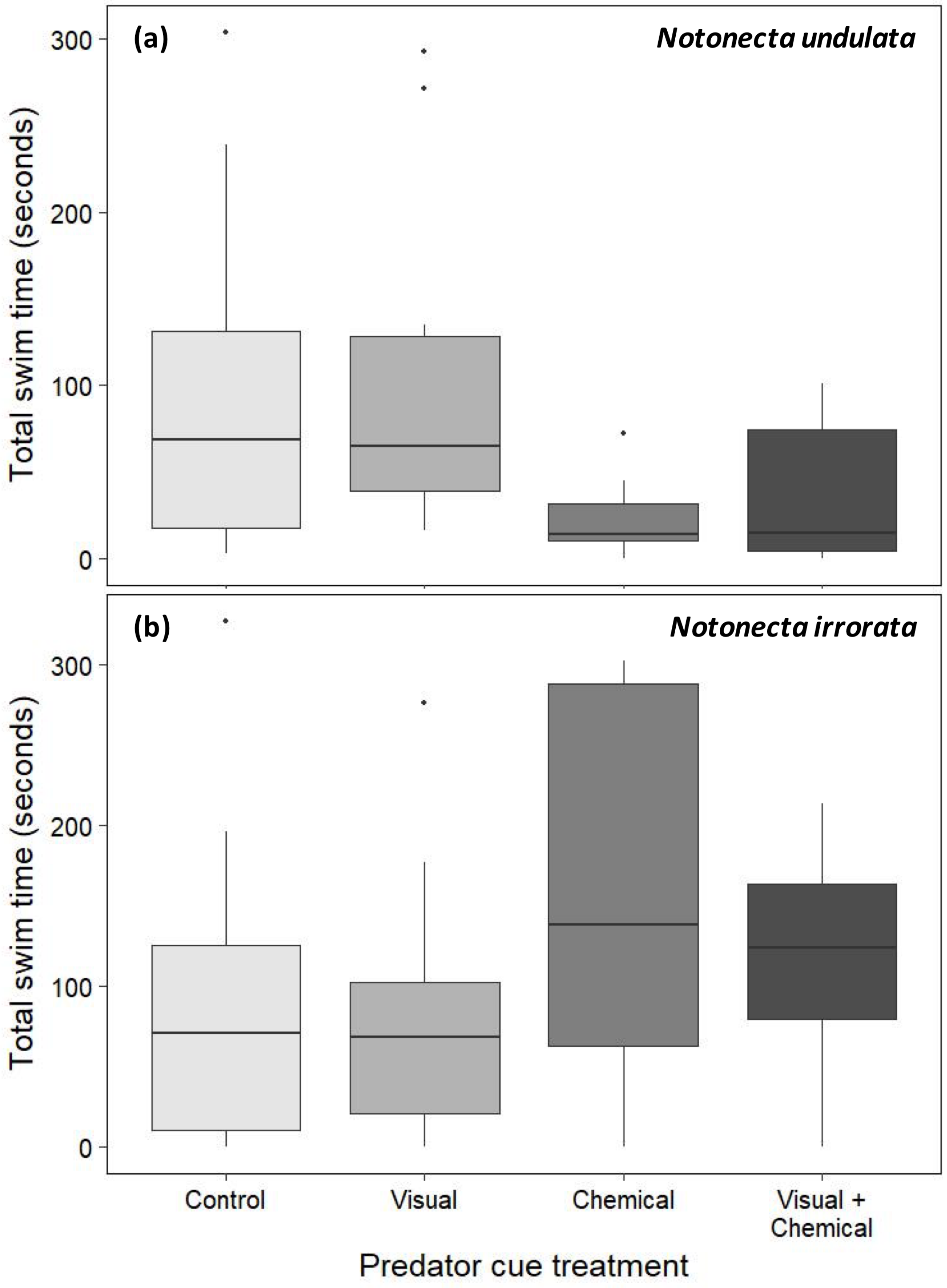
## Figure captions

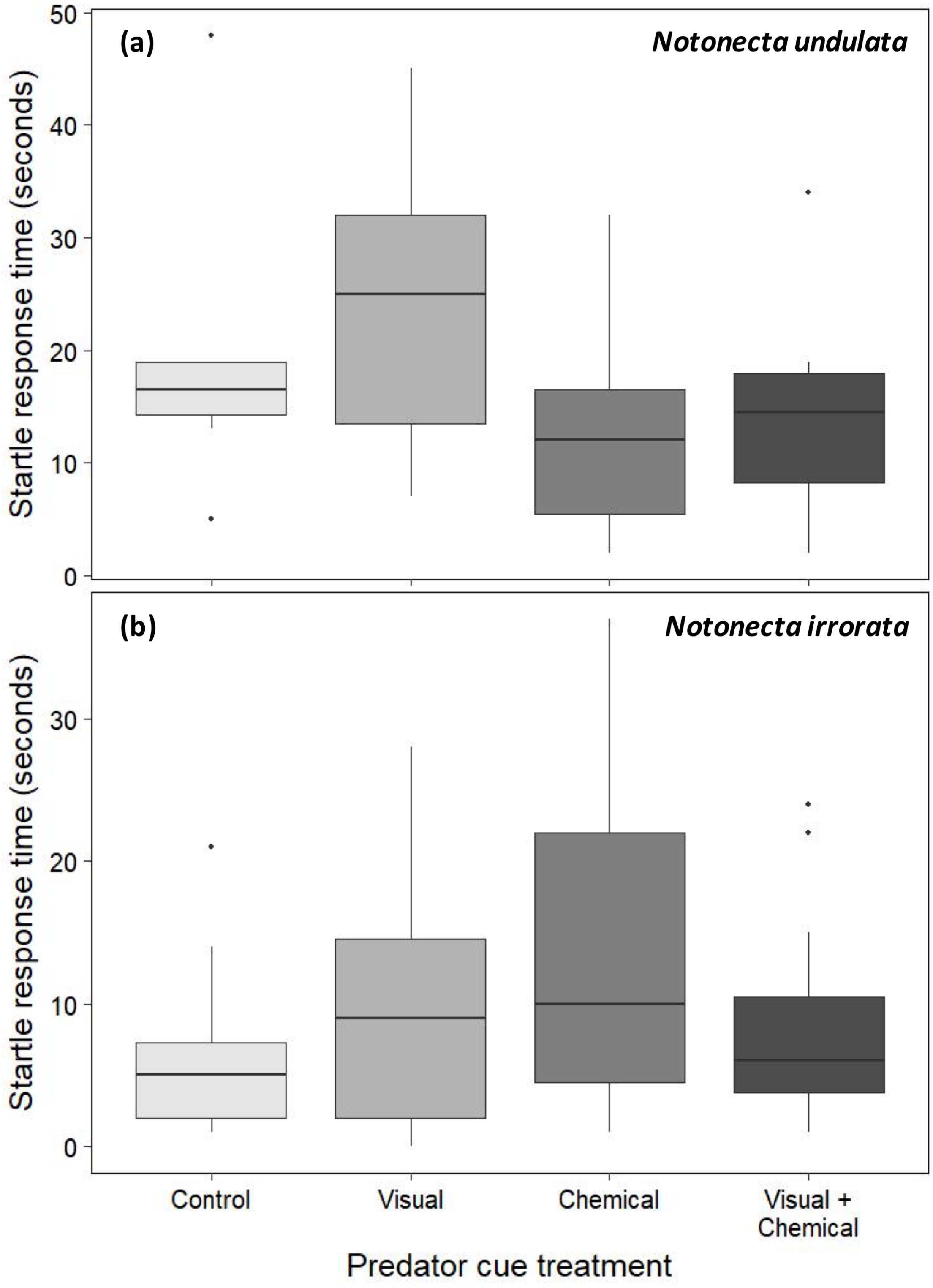
**Fig. 1.** Predator cue treatments containing a predator chamber in the center with one *Notonecta* randomly assigned to each treatment. Dotted predator chambers in (a) and (c) indicate chambers that were perforated with holes. The dark blue portion of the lid in (b) represents the duct tape seal used to exclude any chemical cues. Not pictured: Dried reeds floating at the surface and rocks at the bottom of the predator chamber.

**Fig. 2.** Behavioral responses in swimming activity (total swim time) to belostomatid predator cue treatment for each notonectid congener; (a) *Notonecta undulata* and (b) *Notonecta irrorata*. *N. undulata* exhibit behavioral plasticity to chemically-mediated predator cues, but *N. irrorata* does not exhibit any plasticity to nonlethal predator cues.

**Fig. 3.** Behavioral responses following a startle stimulus (startle response time) to mimic predation attack when exposed to cues of the belostomatid predator for each notonectid congener; (a) *Notonecta undulata* and (b) *Notonecta irrorata*. *N. undulata* exhibit a chemically-mediated change in swimming behavior following a startle stimulus when exposed to non-lethal predator cues, but *N. irrorata* does not exhibit any behavioral plasticity in startle response to the various nonlethal predator cue treatments.


(a)
(c)
(b)
(d)


(a)
*Notonecta undulata*
(b)
*Notonecta irrorata*
Total swim time (seconds)
0
100
200
300
Control
Visual
Chemical
Visual + Chemical
Predator cue treatment


(a)
Notonecta undulata
(b)
Notonecta irrorata
Startle response time (seconds)
0
10
20
30
40
50
Control
Visual
Chemical
Visual + Chemical
Predator cue treatment