Phyllomedusa 23(1):55–64, 2024
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ISSN 1519-1397 (print) / ISSN 2316-9079 (online)
doi: http://dx.doi.org/10.11606/issn.2316-9079.v23i1p55-64

Behavioral responses of tadpoles of *Sphaerotheca breviceps* (Dicroglossidae), *Duttaphrynus melanostictus* (Bufonidae), and *Polypedates maculatus* (Rhacophoridae) to kairomones and dietary cues of a rare insect predator, *Ranatra elongata* (Nepidae)

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Abstract

Behavioral responses of tadpoles of *Sphaerotheca breviceps* (Dicroglossidae), *Duttaphrynus melanostictus* (Bufonidae), and *Polypedates maculatus* (Rhacophoridae) to kairomones and dietary cues of a rare insect predator, *Ranatra elongata* (Nepidae). Tadpoles of three sympatric anuran species, *Sphaerotheca breviceps, Duttaphrynus melanostictus,* and *Polypedates maculatus,* use chemoreception to detect kairomonal cues and excretory metabolites from active predatory anuran tadpoles (*Hoplobatrachus tigerinus*) that consume them. Herein, we describe the behavioral responses of tadpoles of these three species to a rare sit-and-wait predatory insect, the nepid *Ranatra elongata*. The predator's kairomones (water conditioned by a starved predator) or kairomones + diet-derived metabolites (dietary cues released in excreta of the predator after consumption of conspecific prey tadpoles) were used to simulate predation risk. Tadpoles of the three species had no behavioral responses to predator kairomones. However, all three species drastically reduced swimming movements and overall time spent swimming and had a higher burst speed/swimming velocity in response to water-borne cues released from the excreta of predators fed conspecific prey items. Because the presence of *R. elongata* does not elicit defense behaviors in tadpoles of these three prey species, additional information related to digestion of conspecifics is required to elicit defensive behaviors, suggesting that the presence of kairomones is not sufficient to elicit defense behavior.

Keywords: Anuran tadpoles, Chemoreception, Defense behavior, Predation threat, Predator-prey interactions, Reduced activity, Sit-and-wait predators.

Resumo

Respostas comportamentais de girinos de *Sphaerotheca breviceps* (Dicroglossidae), *Duttaphrynus melanostictus* (Bufonidae) e *Polypedates maculatus* (Rhacophoridae) a cairomônios e sinais dietéticos de um inseto predador raro, *Ranatra elongata* (Nepidae). Os girinos de três espécies

Received 09 October 2023
Accepted 25 May 2024
Distributed June 2024

simpátricas de anuros, *Sphaerotheca breviceps, Duttaphrynus melanostictus* e *Polypedates maculatus,* usam a quimiorrecepção para detectar sinais de cairomônios e metabólitos excretórios de girinos predadores ativos de anuros (*Hoplobatrachus tigerinus*) que os consomem. Neste trabalho, descrevemos as respostas comportamentais dos girinos dessas três espécies a um raro inseto predador do tipo senta-e-espera, o nepídeo *Ranatra elongata.* Os cairomônios do predador (água condicionada por um predador faminto) ou cairomônios + metabólitos derivados da dieta (sinais dietéticos liberados na excreta do predador após o consumo de presas coespecíficas) foram usados para simular o risco de predação. Os girinos das três espécies não apresentaram respostas comportamentais aos cairomônios do predador. No entanto, todas as três espécies reduziram drasticamente os movimentos de natação e o tempo total gasto nadando e tiveram uma maior velocidade de explosão/velocidade de natação em resposta a sinais transportados pela água e liberados da excreta de predadores alimentados com presas coespecíficas. Como a presença de *R. elongata* não provoca comportamentos de defesa nos girinos dessas três espécies de presas, informação adicional relacionada à digestão de coespecíficos é necessária para eliciar comportamentos defensivos, sugerindo que a presença de cairomônios não é suficiente para provocar comportamentos de defesa.

Palavras-chave: Atividade reduzida, Comportamento defensivo, Girinos, Interações predador-presa, Predadores senta-e-espera, Quimiorrecepção, Risco de predação.

Introduction

In nature, predation is a major selective force that acts on prey to drive the evolution of strategies for assessment of predation risk and the development of antipredator defense strategies in order to optimize survival and fitness. Detection of predators before an encounter can give prey the opportunity to respond behaviorally and reduce the probability of being detected, and hence eaten (Lima and Dill 1990). Inducing anticipatory antipredator behavior has direct energetic costs, in addition to costs associated with reduced opportunity to feed, that affect growth and development of prey (Lima and Dill 1990, Ferrari *et al.* 2010). The majority of aquatic animals including anuran larvae assess predation risk by using chemosensory mechanisms before responding with defense behaviors (Kats and Dill 1998, Saidapur *et al.* 2009, Ferrari *et al.* 2010, Mogali *et al.* 2012, 2015, Mogali 2018). Anuran larvae specifically perceive either alarm cues released by damaged prey tadpoles or kairomones of predators (chemicals originating from the body of predators) or dietary cues of predators (excretory metabolites or substances of predators fed conspecific prey) to alter behavior to avoid or escape predation (Wisenden 2000, Kiesecker *et al.* 2002, Schoeppner and Relyea 2009a, b, Mogali *et al.* 2011, Carlson *et al.* 2015, Scherer and Smee 2016). Previous studies have revealed that anuran larvae utilize a variety of antipredatory behaviors in response to chemical cues of predators. Those responses include increased activity or swimming speed to escape from predators (Hews 1988, Van Buskirk and McCollum 2000, Dayton *et al.* 2005, Mogali *et al.* 2021), reduction of activity (Skelly and Werner 1990, Mogali *et al.* 2012), aggregation (Spieler and Linsenmair 1999), and increased use of refuge sites (Hossie and Murray 2010, Mogali *et al.* 2019, 2022, 2023c).

In South India, most anurans, including the present study species, *Sphaerotheca breviceps* (Schneider, 1799), *Duttaphrynus melanostictus* (Schneider, 1799), and *Polypedates maculatus* (Gray, 1830), breed in ephemeral ponds following the Southwest monsoon rains. Tadpoles of several sympatric species coexist (Saidapur 2001, Mogali *et al.* 2017, Mogali 2018). Some of these are carnivorous and even cannibalistic, devouring coexisting tadpoles. For example, tadpoles of the Indian bullfrog

Hoplobatrachus tigerinus (Daudin, 1802) are voracious predators that hunt actively; they also exhibit cannibalism (Saidapur 2001, Rajput *et al.* 2011). The ponds in this region harbour many predatory aquatic invertebrates such as beetles (e.g., *Dineutus* sp., *Eretes sticticus*), dragonfly larvae (e.g., *Pantala flavescens*, *Bradinopyga geminata*), damselfly larvae (e.g., *Ceriagrion cerinorubellum*), backswimmers (e.g., *Notonecta* sp.), crabs (e.g., *Barytelphusa* sp.), giant water bugs (e.g., *Belostoma* sp.) and water scorpions (e.g., *Ranatra elongata*). Of these, water scorpions, *Ranatra elongata* (Hemiptera; Nepidae), are interesting and rare tadpole predators that climb among aquatic vegetation, slowly moving near the surface or hiding unnoticed in debris or leaf litter (pers. obs.).

Water scorpions are ambush or sit-and-wait non-gape-limited predators with excellent vision. They are inconspicuous or camouflaged within the vegetation and ambush unsuspecting prey (e.g., tadpoles, water boatmen, and other insects) with a quick grasping action of the forelegs (pers. obs.). They use a segmented beak to pierce prey and suck the body fluids. They capture small to large tadpoles by quickly grabbing and immobilizing them using the front pair of raptorial legs. Tadpoles of *S. breviceps, D. melanostictus,* and *P. maculatus* detect kairomones of tadpoles of *H. tigerinus*, as well as dietary metabolites or substances from predators that have fed on conspecific tadpoles (Saidapur *et al.* 2009, Mogali *et al.* 2011, 2023a, b, d, 2024). The present study examines antipredator behavioral responses of tadpoles of these three species in the presence of sit-and-wait individuals of *R. elongata*. Such studies shed light on predator–prey relations and the diversity of antipredator behavioral responses in tadpoles.

Materials and Methods

Tadpoles of *Sphaerotheca breviceps* [Gosner stages 26–27; *N* = 100; 21.30 ± 0.54 mm total length (mean ± SE); Gosner 1960], *Duttaphrynus melanostictus* (stages 27–28; *N* = 100; 21.27 ± 0.49 mm total length), and *Polypedates maculatus* (stages 26–27; *N* = 100; 21.33 ± 0.58 mm total length) were collected from the same temporary ponds on the Karnatak University Campus, Dharwad (15.44° N, 74.98° E), Karnataka State, India. In the laboratory, tadpoles of each species were placed in separate glass aquaria (75 × 45 × 15 cm) containing 20 L of aged tap water and used as stock for experiments. Tadpoles of the three species are herbivores and were fed boiled spinach. Individuals of *Ranatra elongata* (mean length 75.20 ± 0.68 mm, width 4.5 ± 0.22 mm, and weight 280.0 ± 3.85 mg; *N* = 30) were obtained from the same site as the tadpoles. Predators were reared individually to avoid cannibalism. They were housed in small plastic tubs (19 cm diameter and 7 cm deep) filled with 0.5 L of aged tap water. They were fed with tadpoles of either *S. breviceps, D. melanostictus,* or *P. maculatus*.

Behavioral responses of tadpoles of each prey species were studied by exposing them to stimulus solutions of either predator kairomones alone or kairomones + dietary cues (dietary metabolites of predators fed conspecific tadpoles).

Preparation of Kairomones

Individuals of *R. elongata* were placed in separate plastic tubs (*N* = 25 tubs; 19 cm diameter and 7 cm depth) containing 200 mL of aged tap water without food for 96 h to eliminate diet-derived excretory metabolites from the stimulus solution, resulting in a stimulus solution with only kairomones (Mogali *et al.* 2012, 2020). After 96 h of starvation, predators were removed from the tubs, and the stimulus solutions were further filtered using fine cheese cloth to completely remove any fecal matter. The solutions, containing only kairomones, were used immediately for experimental trials.

Preparation of Dietary Cues of Conspecific Origin and of a Predator Fed Tadpoles of S. breviceps

A single *R. elongata* was placed in a plastic tub (*N* = 8 tubs; 19 cm diameter and 7 cm depth) with 200 mL of aged tap water with four tadpoles of *S. breviceps* in Gosner stages 26–27 (around 08:30 h). *Ranatra elongata* consumed all tadpoles provided to them by evening (18:30 h). The following day between 09:30 h and 11:30 h, predators were removed and water from the tubs was filtered using fine cheese cloth. The filtrate served as the stimulus solution containing the diet-derived excretory metabolites of predators fed conspecific prey, and may contain some extent of kairomones of predators, and are unlikely to have contained the alarm cues of prey. Prey alarm cues are known to be labile in nature (Peacor 2006, Ferrari *et al.* 2008, Wisenden *et al.* 2009, Chivers *et al.* 2013). It is unlikely that prey alarm cues were present in the stimulus solution because all prey were consumed more than 15 h before the solution was collected. The same protocol was followed for dietary cues of the other two species.

Behavioral Responses of Prey Species to the Predator's Kairomones

Behavioral responses of tadpoles of different species to kairomones (water conditioned with starved predators) were recorded by placing one test tadpole (either *S. breviceps, D. melanostictus, P. maculatus*) in a rectangular glass tank (28 × 15 × 15 cm) containing 600 mL of aged tap water. A video camera (Sony, DCR-SR300/E) was fixed above the tank to record tadpoles in the entire tank. The camera was connected to a computer with the Ethovision Video Tracking System (Noldus Information Technology, The Netherlands) to track movements of the tadpole before and after addition of the stimulus solution to the test tank. The Ethovision system was used to record maximum swimming speed (V_{max}), distance traversed by the tadpole, number of swimming bouts, and time spent swimming during an entire trial.

For each trial, one test tadpole was first introduced into the tank and left undisturbed for 5 min. A burette was placed ~1 cm above the water level, and 50 mL of aged tap water (chemical blank solution) was added at the rate of ~1 mL/s. The burette was removed. Movement of the test tadpole was recorded for 5 min using Ethovision to record its baseline activity in the absence of any cues. After tracking baseline activity, 50 mL of stimulus solution containing kairomones was added as described above. Movement of the tadpole was recorded for another 5 min to determine the activity pattern after exposure to kairomones. For tadpoles of each species, 25 trials were conducted (3 species × 25 trials = 75 trials in total). Data on the behavioral responses of tadpoles of different species before and after addition of the stimulus solution (kairomones) were compared separately by using the Paired-Samples t-test (SPSS v. 16.0).

Behavioral Responses of Prey Species to Dietary Cues of Conspecific Origin (Kairomones + Dietary Cues)

In this experiment, the stimulus solution contained chemical cues from excretory metabolites or substances of *R. elongata* fed with conspecifics (kairomones + dietary cues) i.e., either with tadpoles of *S. breviceps, D. melanostictus,* or *P. maculatus* instead of only kairomones of the predator. The behavioral responses of tadpoles of each species were recorded separately as described above, before and after the addition of stimulus solutions that included their respective conspecific prey (kairomones + dietary cues). For each species, 25 trials were conducted. The data on the behavioral responses of tadpoles of different species, before and after addition of the stimulus solution (dietary cues of predators fed with conspecifics) were compared separately using the Paired-Samples t-test (SPSS v. 16.0). All experimental trials were run using a new healthy test tadpole each time. The test tank was cleaned thoroughly and replenished with aged tap water between trials.

Results

Behavioral Responses of Prey Species to Predator's Kairomones

V_{max}, frequency of swimming bouts, time spent swimming, and total distance traversed by tadpoles of *S. breviceps* (Figure 1), *D. melanostictus* (Figure 2), and *P. maculatus* (Figure 3) exposed to chemical blank water were similar to those exposed to kairomones.

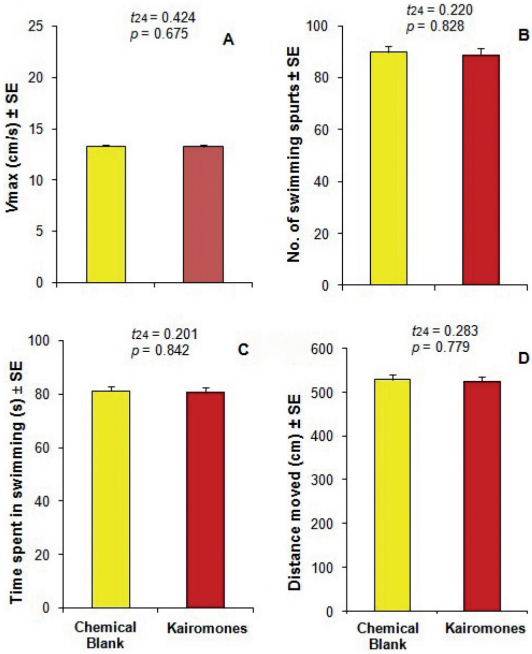

Figure 1. Maximum swimming speed (V_{max}) (**A**), swimming bouts (**B**), time spent swimming (**C**), and distance moved (**D**) by tadpoles of *Sphaerotheca breviceps* exposed to chemical blank water (aged tap water) or a stimulus solution of a starved predator (kairomones), *Ranatra elongata*. Data are represented as mean ± SE; *N* = 25 trials; data analyzed by Paired-Samples t-test.

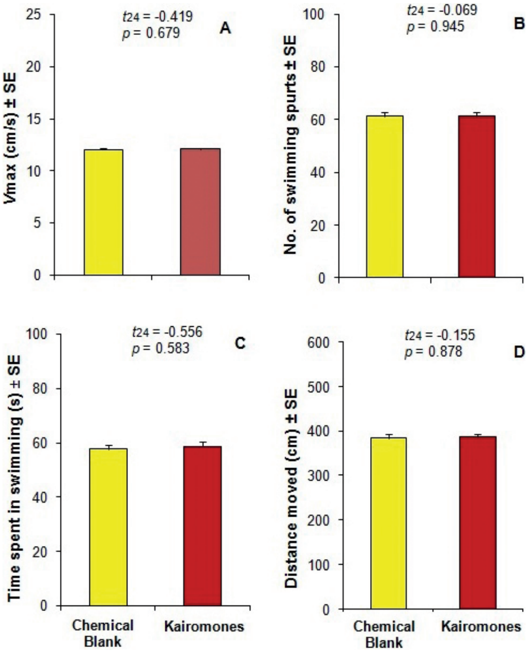

Figure 2. Maximum swimming speed (V_{max}) (**A**), swimming bouts (**B**), time spent swimming (**C**), and distance moved (**D**) by tadpoles of *Duttaphrynus melanostictus* exposed to chemical blank water (aged tap water) or a stimulus solution of a starved predator (kairomones), *Ranatra elongata*. Data are represented as mean ± SE; *N* = 25 trials; data analyzed by Paired-Samples t-test.

Behavioral Responses of Prey Species to Dietary Cues of Conspecific Origin (Kairomones + Dietary Cues)

Upon exposure to the predator' diet-derived metabolites following consumption of conspecific prey (kairomones + dietary cues), tadpoles of *S. breviceps* (Figure 4), *D. melanostictus* (Figure 5), and *P. maculatus* (Figure 6) showed a significant increase in V_{max} and significant declines in the number of swimming bouts, time spent swimming, and total distance moved when compared to their baseline activities in stimulus-free water.

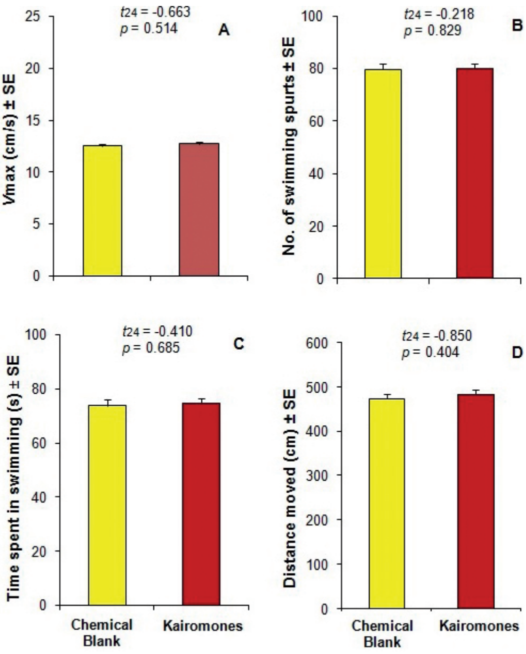

Figure 3. Maximum swimming speed (V_{max}) (**A**), swimming bouts (**B**), time spent swimming (**C**), and distance moved (**D**) by tadpoles of *Polypedates maculatus* exposed to chemical blank water (aged tap water) or a stimulus solution of a starved predator (kairomones), *Ranatra elongata*. Data are represented as mean ± SE; *N* = 25 trials; data analyzed by Paired-Samples t-test.

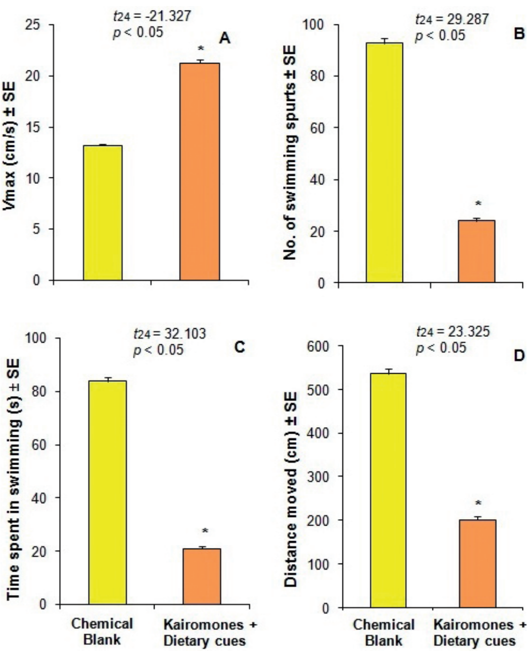

Figure 4. Maximum swimming speed (V_{max}) (**A**), swimming bouts (**B**), time spent swimming (**C**), and distance moved (**D**) by tadpoles of *Sphaerotheca breviceps* exposed to chemical blank water (aged tap water) or a stimulus solution (kairomones + dietary cues) of a nepid predator, *Ranatra elongata,* fed with conspecific tadpoles. Data are represented as mean ± SE; *N* = 25 trials; data analyzed by Paired-Samples t-test. Asterisks over the bars indicate significant differences between the treatment groups.

Discussion

In aquatic ecosystems, most prey organisms, including anuran tadpoles, are at risk of predation (Lima and Dill 1990, Kats and Dill 1998). In such systems, various types of chemical cues (e.g., kairomones, alarm, dietary, and disturbance cues) affect the behavioral responses of tadpoles (Wilson and Lefcort 1993, Schoeppner and Relyea 2005, Scherer and Smee 2016, Rivera-Harnández *et al.* 2022). Anuran larvae are able to discriminate different chemical cues and exhibit differential antipredator behavioral responses according to perceived levels of threat (Mogali *et al.* 2011, 2023b).

The present study shows that tadpoles of three prey species (*S. breviceps, D. melanostictus,* and *P. maculatus*) do not exhibit behavioral changes in response to kairomones of the relatively rare nepid predator, *R. elongata*. This result suggests that they do not perceive cues from *R. elongata* as a predation threat sufficient to elicit the behavioral responses we tested. Similar results were reported for tadpoles of *Indosylvirana temporalis* (Mogali *et al.* 2012), *D. melanostictus* (Mogali *et al.* 2020), and *Clinotarsus curtipes* (Mogali *et al.* 2023d).

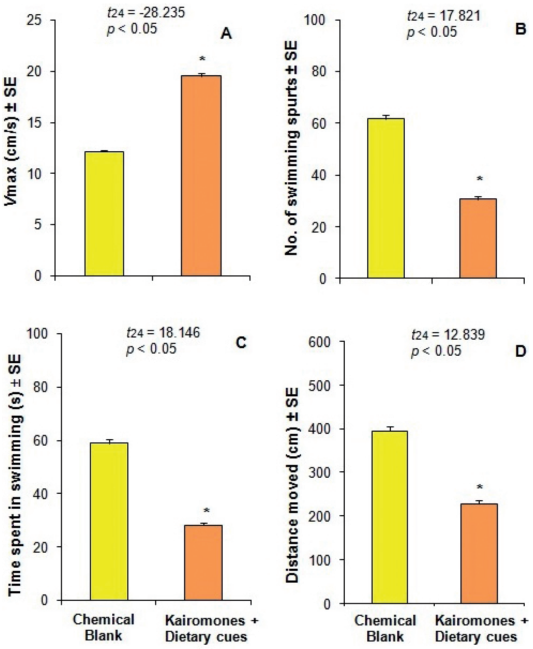

Figure 5. Maximum swimming speed (V_{max}) (**A**), swimming bouts (**B**), time spent swimming (**C**), and distance moved (**D**) by tadpoles of *Duttaphrynus melanostictus* exposed to chemical blank water (aged tap water) or a stimulus solution (kairomones + dietary cues) of a nepid predator, *Ranatra elongata,* fed with conspecific tadpoles. Data are represented as mean ± SE; $N = 25$ trials; data analyzed by Paired-Samples t-test. Asterisks over the bars indicate significant differences between the treatment groups.

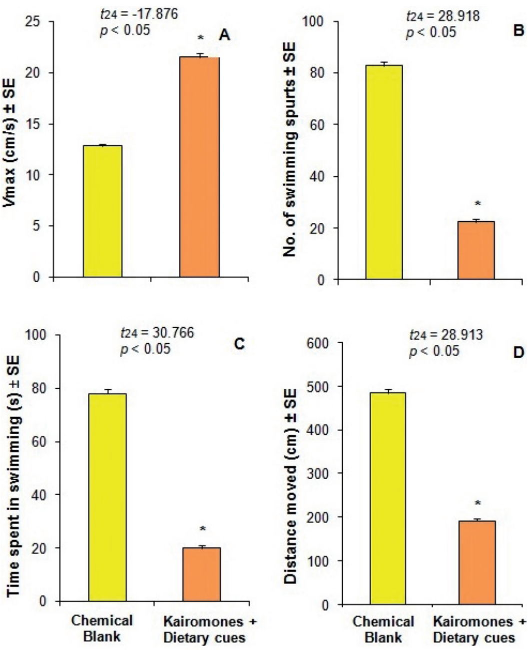

Figure 6. Maximum swimming speed (V_{max}) (**A**), swimming bouts (**B**), time spent swimming (**C**), and distance moved (**D**) by tadpoles of *Polypedates maculatus* exposed to chemical blank water (aged tap water) or a stimulus solution (kairomones + dietary cues) of a nepid predator, *Ranatra elongata,* fed with conspecific tadpoles. Data are represented as mean ± SE; $N = 25$ trials; data analyzed by Paired-Samples t-test. Asterisks over the bars indicate significant differences between the treatment groups.

In contrast, tadpoles of the three species (*S. breviceps, D. melanostictus,* and *P. maculatus*) exhibit strong behavioral changes (i.e., drastically reduced swimming movements and high burst speed) when exposed to kairomones of predatory sympatric tadpoles of *H. tigerinus* (Mogali *et al.* 2011, 2023a, 2024). Tadpoles of *H. tigerinus* locate prey by means of both visual and chemical senses (Saidapur *et al.* 2009). They are active predators, and prey on co-occurring sympatric anuran tadpoles (Saidapur 2001, Saidapur *et al.* 2009). Species such as *H. tigerinus* thus pose a serious predation threat. A long ecological coexistence of tadpoles of these three species with sympatric carnivorous tadpoles such as *H. tigerinus* may have led to the evolution of antipredator defense strategies in response to kairomones of these predators. In contrast, the nepid *R. elongata* is a sit-and-wait predator that moves slowly and waits for prey to come near before attacking (Miller *et al.* 2014). It is possible that *R. elongata* poses less predation risk to these three species than *H. tigerinus*, or that other behavioral responses not measured here are used to evade predation from this different attack strategy. Sit-and-wait predators in general are under intense selection pressure to suppress chemical (e.g., kairomones) evidence of their presence (Miller *et al.* 2015), because they need prey to closely approach them. Also, it is possible that predation pressure by *R. elongata* on these species of tadpoles may be low. If so, tadpoles of these species might be better off conserving their energy by not engaging in antipredator defenses in response to kairomones, if any, of *R. elongata*. On the other hand, water-soluble substances in the excreta of *R. elongata* following consumption of conspecific prey (kairomones + dietary cues) seems to indicate intense predation threat and elicited strong behavioral changes in the three tadpole species in the form of overall reduced swimming movements and high burst speed. Evidence of recent predation on conspecific members of the group indicates a high predation risk for tadpoles in the vicinity. Our results are in agreement with those reported for tadpoles of *Hyla versicolor* (Schoeppner and Relyea 2009b).

Some previous evidence indicates that alarm cues can quickly degrade in nature (Peacor 2006, Ferrari *et al.* 2008, Wisenden *et al.* 2009, Chivers *et al.* 2013). In the present study, given the 15 h time window, it is unlikely. This idea has not been tested in this system, but in other systems involving fish, the effect of cues in eliciting defensive behavior lasted for 6 h (Wisenden *et al.* 2009), whereas in larval woodforgs, the cues lasted 2 h (Ferrari *et al.* 2008). The antipredator defense behavior of the three tadpole species in the present study was specifically in response to diet-derived excretory metabolites or substances released by *R. elongata* that have consumed conspecific prey items. In conclusion, kairomones are not sufficient to induce defensive behavior but require the addition of diet-derived metabolites. The three tadpole species in this study can exhibit different behavioral responses to different predator-related cues.

Acknowledgments

The study was supported by a grant from the Department of Science and Technology, New Delhi (No. SP-SO/AS-38/2009) awarded to BAS. SMM was supported as project assistant in the project. All work reported herein was conducted in accordance with ethical guidelines according to CPCSEA, New Delhi, India (registration no. 639/02/a/CPCSEA).

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Editor: Ross Alford