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Behavioural responses of predator-naïve, predator-experienced and wild-caught *Sphaerotheca breviceps* tadpoles to kairomones from the carnivorous tadpoles of *Hoplobatrachus tigerinus*

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Abstract. The behavioural responses of predator-naïve (laboratory-born), predator-experienced (laboratory-born but with short-term experience with predators), and wild-caught (with long-term experience with predators in natural settings) tadpoles of *Sphaerotheca breviceps* to carnivorous predatory tadpoles of *Hoplobatrachus tigerinus* was studied in the laboratory. The predator's stimulus solution (kairomones) was used to simulate predation threat. All *S. breviceps* tadpoles (i.e., predator-naïve, predator-experienced and wild-caught) exhibited behavioural antipredator responses, i.e., reduced swimming activity and time spent swimming, and had a higher burst speed in response to water-borne kairomonal cues of predators. Wild-caught tadpoles showed stronger responses than predator-naïve and predator-experienced tadpoles and the latter exhibited stronger responses than predator-naïve tadpoles. Our study thus suggests that antipredator behaviour in these tadpoles is basically innate. Furthermore, the enhanced antipredator behaviour of wild-caught tadpoles indicates that learning is involved.

Key words. Amphibia, Anura, antipredator behaviour, chemical cues, prey, predator, tadpole.

Introduction

Predator-prey interactions play a vital role in shaping the life-history strategies of animals. Predation is a chief selection pressure forcing prey animals to maximize their fitness by recognizing and avoiding predators also in aquatic systems (Lima & Dill 1990). Thus, predators can impact on behaviour, morphology and the life history of individuals and populations of preyed species (Lima & Dill 1990, Laforsch & Tollrian 2004, Ferrari et al. 2010). For predator recognition, prey animals may use wide array of cues, e.g., visual, acoustic, electric, tactile, disturbing, chemical or a combination thereof (Amo et al. 2004, McCormick & Manassa 2007, Ferrari et al. 2010, Mogali et al. 2012, Landeira-Dabarca et al. 2019). In aquatic predator–prey systems, chemical cues are considered particularly important, as these can usually be detected over larger distances than, e.g., visual cues (Chivers et al. 1996).

Anuran tadpoles make for an excellent model system for studying predator–prey interactions because they are highly vulnerable to aquatic predators (Heyer et al. 1975, Gascon 1992). Previous studies suggest that the tadpoles of most species assess predation risks using chemosensory mechanisms before responding with defence behaviours (Ferrari et al. 2010, Mogali et al. 2011a, 2012). In particular, they are attuned to alarm substances released by injured prey, kairomones of predators, and dietary cues to alter their behaviour and so escape predation (Schoeppner & Relyea 2005, 2009, Mogali et al. 2012, 2023a, b, c, Scherer & Smee 2016). Previous studies have also revealed that tadpoles exhibit a variety of antipredator behaviours to chemical cues of predators, including reduced activity levels (Mogali et al. 2011a), high swimming speed in order to outrun predators (Mogali et al. 2021), increased use of hiding spots (Hossie & Murray 2010, Mogali et al. 2022), aggregation (Spieler & Linsenmair 1999), and others.

The Indian Burrowing Frog, *Sphaerotheca breviceps* (Schneider, 1799), is widely distributed in India. In south India, during the early monsoon season, it generally breeds in ephemeral water bodies in sympatry with other anuran species (Mogali et al. 2011b, 2023a). Offering the herbivorous growth the tadpoles of *S. breviceps* require as food, these ephemeral water bodies are also home to a variety of predators, mainly insects, omnivorous predatory tadpoles like those of *Euphlyctis cyanophlyctis* (Schneider, 1799), and the carnivorous predatory tadpoles of *Hoplobatrachus tigerinus* (Daudin, 1802) (pers. obs.). During our regular field visits, we noticed that the tadpoles of *S. breviceps* are preyed upon by a variety of predators, but mainly are actively hunted by the carnivorous tadpoles of *H. tigerinus*. Most previous tadpole prey–predator interaction studies have focused on aquatic insects, fishes, or salamanders as predators (Chivers & Mirza 2001, Mathis 2003, Mogali et al. 2022), and so far there seems to be a paucity of research investigating the effects of predatory tadpoles on the behavioural responses of herbivorous tadpoles. More importantly, most previous studies looked at the behavioural responses of prey tadpoles by using either only laboratory-raised (predator-naive) or laboratory-raised ones with short-term (few hours) experience with predators (predator-experienced), or tadpoles with long-term experience with predators in natural settings (wild-caught) and the role of chemical cues of predators.

In the present work, we studied systematically the behavioural responses of predator-naive, predator-experienced and wild-caught *S. breviceps* tadpoles to the stimulus solution (kairomones) of their natural predator, *H. tigerinus*. We hypothesized that all three types of prey tadpoles should principally exhibit behavioural antipredator responses to the kairomones of that predator. We also hypothesized that both predator-experienced and wild-caught tadpoles should display more enhanced behavioural antipredator responses to predators than would predator-naïve tadpoles as they already have previously had some experience with predators. Additionally, we hypothesized that wild-caught tadpoles should exhibit the strongest behavioural antipredator responses, as they should draw from their long-term experience with predators in natural settings. Thus, the outcome of this study will provide novel information in the field of behavioural ecology of anuran tadpoles with especial reference to the prey–predator interactions between the species involved.

Material and methods

Four egg clutches of *Sphaerotheca breviceps* were collected from an ephemeral pond in the Karnatak University Campus, Dharwad, Karnataka State, India (latitude 15.44041° N, longitude 74.98525° E), in the early monsoon period in May of 2011 and immediately transported to the laboratory. They were placed separately in plastic tubs (32 cm diameter and 14 cm depth), each containing 5 l of aged (dechlorinated) tap water. The eggs from all four clutches hatched synchronously at Gosner stage 19 (Gosner 1960) the next day. The tadpoles from all four clutches were then mixed to normalize genetic differences between the groups and were raised together (50 tadpoles from each clutch × 4 egg clutches = 200 tadpoles) in a glass aquarium (90 × 30 × 15 cm, lwh) containing 20 l of aged tap water. Two such stocks were maintained (i.e., 400 tadpoles in total). Five days prior to the experimental trials, predatory tadpoles of *H. tigerinus* (Gosner stages 33–34; mean total length 38.15 ± 1.17 mm, N = 20) and prey tadpoles of *S. breviceps* (Gosner stages 31–32; mean total length 28.50 ± 1.87 mm, N = 50) were collected from the same pond (a natural water body) from which the eggs of *S. breviceps* had been obtained. The tadpoles of *H. tigerinus* were raised individually to prevent cannibalism, housing them in plastic tubs (19 cm diameter and 7 cm depth) containing 0.5 l of aged tap water. All tadpoles were kept at room temperature at 25°C and exposed to the natural photoperiod (12 h light, 12 h dark). The tadpoles of *S. breviceps* are herbivorous by nature, hence they were fed with boiled spinach ad libitum. Those of *H. tigerinus* are carnivorous by nature, hence they were fed with surplus *S. breviceps* tadpoles. The tadpoles of *S. breviceps* that developed or were raised in the laboratory from egg stage are here termed predator-naïve tadpoles, whereas those that likewise developed in the laboratory but were then exposed to predators for a short period (8 h) are termed predator-experienced tadpoles. Tadpoles of *S. breviceps* that were obtained from their natural habitat and therefore could be supposed to have had long-term experience with predators for a minimum period of 15 days are termed wild-caught here. The behavioural responses of all these test tadpoles of *S. breviceps* were studied by exposing them to a "stimulus solution" of kairomones of the predatory tadpoles of *H. tigerinus*.

Preparation of predator stimulus solution (kairomones)

The *H. tigerinus* tadpoles were placed individually in separate plastic tubs (N = 10 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). After 96 h of starving, the tadpoles were removed from the tub and the water containing the stimulus solution was filtered to remove completely any faecal matter possibly present in it and used immediately for experimental trials.

Test subjects (predator-naïve and predator-experienced tadpoles)

A total of 25 tadpoles (Gosner stages 31–32; mean total length 28.65 ± 1.53 mm) that had been raised in the absence of any predators from the time of hatching were placed in plastic tubs (32 cm diameter and 14 cm depth) containing 5 l of aged tap water. Eight such tubs were maintained. A single *H. tigerinus* (Gosner stages 33–34) tadpole that had been starved for 1 day was then introduced to four of these tubs from 09.00 to 17.00 h. On average, the predator consumed 6 ± 0.4 and injured 3 ± 0.3 naïve tadpoles during this 8-h period. The predator and injured tadpoles were then removed. The uninjured but now predator-experienced tadpoles were used for trials on the subsequent day. The test tadpoles of the remaining four tubs (without predators) served as predator-naïve subjects.

Test subjects (wild-caught tadpoles)

Tadpoles of *S. breviceps* (Gosner stages 31–32; mean total length 28.50 ± 1.87 mm, N = 50) were collected from their natural water body from which the eggs of *S. breviceps* and tadpoles of *H. tigerinus* were also obtained. They had lived there for more than 15 days in the company of many aquatic predators including *H. tigerinus* tadpoles. A total of 25 of these wild-caught tadpoles were likewise placed in plastic tubs (32 cm diameter and 14 cm depth) containing 5 l of aged tap water. Two such tubs were maintained.

Behavioural responses

The behavioural responses of *S. breviceps* tadpoles to predator kairomones were recorded by placing a single tadpole of *S. breviceps* (either of predator-naïve or predator-experienced or wild-caught; Gosner stages 31–32) in a glass tank (28 × 15 × 15 cm, lwh) containing 600 ml of chemically pure water. A Sony handycam (DCR-SR300/E) was mounted above the tank so that it recorded the entire area. The handycam was then connected to a computer with the Ethovision Video Tracking System (Noldus Information Technology, The Netherlands) to track the movements of the tadpole before and after stimulus solution was added to the test tank and record some important behavioral parameters such as maximum swimming speed (V_{max}), distance traversed by the tadpole, number of swimming spurts, and time spent swimming during an entire trial. For each trial, a new test tadpole, either predator-naïve or predator-experienced or wild-caught, was introduced to the tank first and left undisturbed for 5 min. A burette was placed ~1 cm above the water level and 50 ml of chemically pure water was then added at a rate of ~1 ml/s to emulate the disturbance that the later chemical cue would make. The burette was then inconspicuously removed. Movement of the tadpole was then recorded for 5 min on the Ethovision system to obtain a reference baseline of its activity in the absence of any cues. After that period, 50 ml of stimulus solution (kairomones) were added with a burette in the manner described above. Movement of the tadpole was recorded for another 5 min to identify its activity pattern after exposure to kairomones.

Twenty-five trials were carried out for each group (75 trials in total). For each trial, a new healthy test tadpole was used. The glass tank was cleaned and replenished with chemically pure water between trials.

Statistical analysis

After checking for normality, the data on the behavioural responses of *S. breviceps* (either predator-naïve, predator-experienced or wild-caught) tadpoles before and after the addition of the stimulus solution containing kairomones of a predator were compared separately by using the paired t-test. The data were analyzed using a general linear model for testing the overall effects of tadpole type (predator-naïve, predator-experienced, wild-caught), treatment type (chemically pure water, with stimulus solution) and their interactions. Also, the data on the behavioural responses between different (i.e., predator-naïve, predator-experienced and wild-caught) *S. breviceps* tadpoles to kairomones of a predator were analyzed by a one-way ANOVA followed by a Tukey's HSD post-hoc test. All these statistical tests were performed using SPSS ver. 16.0.

Results

Behavioural responses of predator-naïve *S. breviceps* tadpoles to kairomones of *H. tigerinus* tadpoles

Upon exposure to predator kairomones, predator-naïve *S. breviceps* tadpoles displayed a significant increase in V_{max} and a significant decrease in the number of swimming spurts, time spent swimming , and total distance moved when compared to their baseline activities in chemically pure water (Table 1A).

Behavioural responses of predator-experienced *S. breviceps* tadpoles to kairomones of *H. tigerinus* tadpoles

Upon exposure to predator kairomones, predator-experienced *S. breviceps* tadpoles showed a significant increase in V_{max}, and a significant decrease in the number of swimming spurts , time spent swimming, and total distance moved when compared to their baseline activities in chemically pure water (Table 1B).

Behavioural responses of wild-caught *S. breviceps* tadpoles to kairomones of *H. tigerinus* tadpoles

Upon exposure to predator kairomones, wild-caught *S. breviceps* tadpoles showed a significant increase in V_{max}, and a significant decrease in the number of swimming spurts , time spent swimming, and total distance moved when compared to their baseline activities in chemically pure water (Table 1C).

Intensity of defence behaviours in *S. breviceps* tadpoles to kairomones of *H. tigerinus* tadpoles

The results of a general linear model showed that both tadpole type and treatment type influenced the swimming activities in *S. breviceps* tadpoles independently and also their interactions (Table 2). Results of the ANOVA indicated that there were significant differences in the V_{max}, number of swimming spurts, time spent swimming, and total distance moved between the prey tadpoles of the different treatment groups (Table 3). The intensity of defence behaviours varied significantly with the prey's experience with the cue. The wild-caught tadpoles exhibited significantly higher V_{max} ($P = 0.000$), spent significantly less time swim-

Table 1. Behavioural responses of predator-naïve, predator-experienced, and wild-caught *Sphaerotheca breviceps* tadpoles to chemically pure water (aged tap water) or stimulus solution (kairomones) of their predator, the larvae of *Hoplobatrachus tigerinus*. Data are represented as means ± SE and analyzed with a Paired-Sample t-test.

A) Predator-naive tadpoles (N = 25 trials)

Treatment	Maximum swimming speed (V_{max}; cm/s)	Frequency of swimming spurts	Time spent swimming (s)	Distance travelled (cm)
Chemically pure water	13.40 ± 0.12	91.80 ± 2.55	82.12 ± 1.65	541.08 ± 8.51
Stimulus solution	21.12 ± 0.33	22.76 ± 0.88	19.32 ± 0.67	194.62 ± 7.62
t-values	t = 21.521, df = 24	t = 26.749, df = 24	t = 33.791, df = 24	t = 31.694, df = 24
P-values	P = 0.000	P = 0.000	P = 0.000	P = 0.000

B) Predator-experienced tadpoles (N = 25 trials)

Treatment	Maximum swimming speed (V_{max}; cm/s)	Frequency of swimming spurts	Time spent swimming (s)	Distance travelled (cm)
Chemically pure water	13.17 ± 0.13	87.52 ± 2.21	80.11 ± 1.88	535.85 ± 10.77
Stimulus solution	23.51 ± 0.25	13.68 ± 0.40	12.04 ± 0.41	140.63 ± 5.87
t-values	t = -38.902, df = 24	t = 32.884, df = 24	t = 35.273, df = 24	t = 31.701, df = 24
P-values	P = 0.000	P = 0.000	P = 0.000	P = 0.000

C) Wild-caught tadpoles (N = 25 trials)

Treatment	Maximum swimming speed (V_{max}; cm/s)	Frequency of swimming spurts	Time spent swimming (s)	Distance travelled (cm)
Chemically pure water	13.28 ± 0.13	90.60 ± 2.29	81.73 ± 1.98	538.68 ± 10.13
Stimulus solution	27.33 ± 0.59	5.52 ± 0.32	4.95 ± 0.32	72.27 ± 4.14
t-values	t = -25.655, df = 24	t = 36.356, df = 24	t = 36.087, df = 24	t = 42.919, df = 24
P-values	P = 0.000	P = 0.000	P = 0.000	P = 0.000

Table 2. Results of a general linear model for overall effects of tadpole type (predator-naïve, predator-experienced, wild-caught), treatment type (chemically pure water, stimulus solution) and their interactions. The response variables are the various swimming activities (maximum swimming speed, frequency of swimming spurts, time spent swimming, and total distances travelled) of *Sphaerotheca breviceps* tadpoles. Significant values are in boldface.

Source	Wilks' lambda	F	P
Tadpole type	0.416	19.373	0.000
Treatment type	0.014	2556.0	0.000
Tadpole type × treatment type	0.431	18.442	0.000

ming (P = 0.000), a reduced number of swimming spurts (P = 0.000), and moved for shorter distances (P = 0.000) compared to all other groups (Table 3). The predator-experienced tadpoles also exhibited significantly higher V_{max} (P = 0.000), spent significantly less time swimming (P = 0.000), reduced number of swimming spurts (P = 0.000), and moved only over short distances (P = 0.000) compared to the predator-naïve and control (chemically pure water) groups (Table 3). The predator-naïve tadpoles exhibited significant higher V_{max} (P = 0.000), spent less time swimming (P = 0.000), engaged in a reduced number of swimming spurts (P = 0.000), and moved only over short distances (P = 0.000) compared to their conspecifics in chemically pure water (Table 3). The hierarchy of the intensity of defence behaviours thus is wild-caught (highest) > predator-experienced (moderate) > predator-naïve tadpoles (lowest) > chemically pure water (control group, Tables 1 and 3).

Discussion

In aquatic systems, many organisms including larval anurans are at a high risk of predation, but the level of their risk is dependent on the effectiveness of their defences, which have evolved to promote their escape from predators and ultimately promote their survival (Schmidt & Amezquita 2001, Relyea 2007). In such systems, various types of chemical cues, e.g., alarm substances of damaged conspecifics, dietary metabolites of predators, disturbances and kairomones of predators affect the behavioural responses of many prey animals including anuran larvae (Schoeppner & Relyea 2005, Mogali et al. 2011a, 2012).

The existence of kairomones (predator odour) that elicit antipredator behaviour in prey has been reported for a wide array of animals (Kats & Dill 1998, Ferrari et al. 2010, Mogali et al. 2011a). Kairomones are generally considered the chemical signatures of predators. A few experimental studies involving starved predators have demonstrated that kairomones will not elicit antipredator behaviour in cer-

Table 3. Behavioural responses of *Sphaerotheca breviceps* tadpoles to chemically pure water and to stimulus solution (kairomones) of its predator, the larvae of *Hoplobatrachus tigerinus*. Data are represented as means ± SE and analyzed by a one-way ANOVA followed by a Tukey's HSD post-hoc test. Dissimilar letters indicate significant differences between treatment groups. Twenty-five trials were conducted with each treatment group.

Treatment	Maximum swimming speed (V_{max}; cm/s)	Frequency of swimming spurts	Time spent swimming (s)	Distance travelled (cm)
Chemically pure water (pooled)	13.28 ± 0.74^{a}	89.97 ± 1.35^{a}	81.32 ± 1.05^{a}	538.53 ± 5.61^{a}
Stimulus solution (kairomones)				
Predator-naïve tadpoles	21.12 ± 0.33^{b}	22.76 ± 0.88^{b}	19.32 ± 0.67^{b}	194.62 ± 7.62^{b}
Predator-experienced tadpoles	23.51 ± 0.25^{c}	13.68 ± 0.40^{c}	12.04 ± 0.41^{c}	140.63 ± 5.87^{c}
Wild-caught tadpoles	27.33 ± 0.59^{d}	5.52 ± 0.32^{d}	4.95 ± 0.32^{d}	72.27 ± 4.14^{d}
F-values	F = 662.70, df = 3,146	F = 985.50, df = 3,146	F = 1337.0, df = 3,146	F = 1266.0, df = 3,146
P-values	P = 0.000	P = 0.000	P = 0.000	P = 0.000

tain prey taxa, though (Crowl & Covich 1990, Stirling 1995, Mogali et al. 2012), whereas a few others, including those on larval anurans, have shown that kairomones induce strong antipredator behaviour (Hazlett & Schoolmaster 1998, Petranka & Hayes 1998, Van Buskirk & Arioli 2002, Schoeppner & Relyea 2005, 2009, Mogali 2018, Mogali et al. 2011a, 2023b, Gyssels & Stoks 2006).

The results of the present study indicates that all three types of tadpoles of *S. breviceps,* i.e., predator-naïve, predator-experienced and wild-caught ones, basically sensed the kairomones of hunting *H. tigerinus* tadpoles and responded by decreasing their activity levels (less time spent in swimming, less distance traversed, and fewer swimming spurts) during the trial period. Furthermore, it is interesting to note that whenever the *S. breviceps* tadpoles moved in the stimulus solution (kairomones) their spurt speed (V_{max}) was higher than in chemically pure water, indicating their efforts to escape the perceived threat of a nearby predator as was implied by the presence of kairomones. Our results conform with earlier studies on *Bufo melanostictus* (Mogali et al. 2011a) and *Polypedates maculatus* tadpoles (Mogali 2018, Mogali et al. 2023b). In contrast, tadpoles of *Rana temporalis* (Mogali et al. 2012) and *B. melanostictus* (Mogali et al. 2020) apparently do not alter their behaviour in response to kairomones from insect predators, such as the larvae of the dragonfly *Pantala flavescens*. This might be because dragonfly larvae are sit-and-wait predators that move slowly and usually wait for prey to come within striking range (Miller et al. 2014). They seem to be perceived as a lower predation threat by the prey. There is intense selection pressure on sit-and-wait predators to suppress chemical evidence (e.g., kairomones) of their presence, because they need the prey to approach them (Miller et al. 2015). The tadpoles of *S. breviceps* exhibited strong behavioural antipredator responses to *H. tigerinus* tadpoles, because the latter actively hunt syntopic anuran tadpoles (Mogali et al. 2011, 2023b). *H. tigerinus* tadpoles therefore pose a serious predation threat to *S. breviceps* tadpoles. The long ecological co-existence of *S. breviceps* tadpoles with sympatric carnivorous tadpoles such as those of *H. tigerinus* may have driven the evolution of antipredator defence strategies in response to the kairomones of these predators.

The results of the present study also clearly demonstrate that wild-caught tadpoles have the strongest behavioural antipredator responses compared to those by predator-experienced and even more so compared to predator-naïve tadpoles. Our experimental study thus indicates that tadpoles of all types basically react to the predator kairomones, suggesting that their antipredator behaviour is innate. The differences between these groups also suggests that some learning is involved – the longer the tadpoles (wild-caught) were in contact with predators or its cues, the stronger they react. Hence, there clearly is a combination of both innate and learned behaviours. Our results are in agreement with earlier studies (Chivers & Ferrari 2013, Crane et al. 2017, Mogali et al. 2023c).

In summary, the present study demonstrates that all *S. breviceps* tadpoles, be they predator-naïve, predator-experienced or wild-caught, exhibit behavioural antipredator responses to kairomones of the predatory tadpoles of *H. tigerinus*.The enhanced antipredator behaviour of wild-caught tadpoles may suggest their long-term experience with predators in natural water bodies.

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References

Amo, L., P. Lopez & J. Martin (2004): Wall lizards combine chemical and visual cues of ambush snake predators to avoid overestimating risk inside refuges. – Animal Behaviour, **67**: 647–653.

Chivers, D. P. & M. C. O. Ferrari (2013): Tadpole antipredator responses change over time: what is the role of learning and generalization? – Behavioral Ecology, **24**: 1114–1121.

Chivers, D. P. & R. S. Mirza (2001): Importance of predator diet cues in responses of larval wood frogs to fish and invertebrate predators. – Journal of Chemical Ecology, **27**: 45–51.

Chivers, D. P., G. E. Brown & R. J. F. Smith (1996): The evolution of chemical alarm signals: attracting predators benefits alarm signal senders. – American Naturalist, **148**: 649–659.

Crane, A. L., B. S. Demuth & M. C. O. Ferrari (2017): Experience with predators shapes learning rules in larval amphibians. – Behavioral Ecology, **28**: 312–318.

Crowl, T. A. & A. P. Covich (1990): Predator-induced life-history shifts in a freshwater snail. – Science, **247**: 949–951.

Ferrari, M. C. O., B. D. Wisenden & D. P. Chivers (2010): Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. – Canadian Journal of Zoology, **88**: 698–724.

Gascon, C. (1992): Aquatic predators and tadpole prey in Central Amazonia: field data and experimental manipulations. – Ecology, **73**: 971–980.

Gosner, K. L. (1960): A simplified table for staging anuran embryos and larvae with notes on identification. – Herpetologica, **16**: 183–190.

Gyssels, F. & R. Stoks (2006): Behavioural responses to fish kairomones and autotomy in a damselfly. – Journal of Ethology, **24**: 79–83.

Hazlett, B. A. & D. R. Schoolmaster (1998): Responses of cambarid crayfish to predator odor. – Journal of Chemical Ecology, **24**: 1757–1770.

Heyer, W. R., R. W. McDiarmid & D. L. Weigmann (1975): Tadpoles, predation and pond habitats in the tropics. – Biotropica, **7**: 100–111.

Hossie, T. J. & D. L. Murray (2010): You can't run but you can hide: refuge use in frog tadpoles elicits density-dependent predation by dragonfly larvae. – Oecologia, **163**: 395–404.

Kats, L. B. & L. M. Dill (1998): The scent of death: chemosensory assessment of predation risk by prey animals. – Ecoscience, **5**: 361–394.

Laforsch, C. & R. Tollrian (2004): Inducible defenses in multimodal environments: cyclomorphosis in *Daphnia cucullata*. – Ecology, **85**: 2302–2311.

Landeira-Dabarca, A., J. Näslund, J. I., Johnsson & M. Álvarez (2019): Cue recognition and behavioural responses in the three-spined stickleback (*Gasterosteus aculeatus*) under risk of fish predation. – Acta Ethologica, **22**: 209–221.

Lima, S. L. & L. M. Dill (1990): Behavioral decisions made under the risk of predation: a review and prospectus. – Canadian Journal of Zoology, **68**: 619–640.

Mathis, A. (2003): Use of chemical cues in detection of conspecific predators and prey by newts, *Notophthamus viridescens*. – Chemoecology, **13**: 193–197.

McCormick, M. I. & R. Manassa (2007): Predation risk assessment by olfactory and visual cues in a coral reef fish. – Coral Reefs, **27**: 105–113.

Miller, J. R. B., J. M. Ament & O. J. Schmitz (2014): Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. – Journal of Animal Ecology, **83**: 214–222.

Miller, A. K., B. Martiz, S. Mckay, X. Glaudas & G. J. Alexander (2015): An ambusher's arsenal: chemical crypsis in the puff adder (*Bitis arietans*). – Proceedings of the Royal Society B: Biological Sciences, **282**: 20152182.

Mogali, S. M. (2018): Predatory cues influence the behavioral responses and metamorphic traits of *Polypedates maculatus* (Anura: Rhacophoridae). – Asian Herpetological Research, **9**: 188–194.

Mogali, S. M., S. K. Saidapur & B. A. Shanbhag (2011a): Levels of predation modulate antipredator defense behavior and metamorphic traits in the toad *Bufo melanostictus*. – Journal of Herpetology, **45**: 428–431.

Mogali, S. M., S. K. Saidapur & B. A. Shanbhag (2011b): Receding water levels hasten metamorphosis in the frog, *Sphaerotheca breviceps* (Schneider, 1799): a laboratory study. – Current Science, **101**: 1219–1222.

Mogali, S. M., S. K. Saidapur & B. A. Shanbhag (2012): Tadpoles of the bronze frog (*Rana temporalis*) assess predation risk before evoking antipredator defense behavior. – Journal of Ethology, **30**: 379–386.

Mogali, S. M., S. K. Saidapur & B. A. Shanbhag (2020): Behavioral responses of tadpoles of *Duttaphrynus melanostictus* (Anura: Bufonidae) to cues of starved and fed dragonfly larvae. – Phyllomedusa, **19**: 93–98.

Mogali, S. M., B. A. Shanbhag & S. K. Saidapur (2021): Comparative vulnerability of *Indosylvirana temporalis* and *Clinotarsus curtipes* (Anura: Ranidae) tadpoles to water scorpions: importance of refugia and swimming speed in predator avoidance. – Phyllomedusa, **20**: 159–164.

Mogali, S. M., B. A. Shanbhag & S. K. Saidapur (2022): Knowledge of predators and accessibility to refuge reduces larval mortality of the Bicolored frog, *Clinotarsus curtipes* (Anura: Ranidae). – Salamandra, **58**: 157–160.

Mogali, S. M., B. A. Shanbhag & S. K. Saidapur (2023a): Similar antipredator behaviour in tadpoles of two closely associated anuran species *Duttaphrynus melanostictus* and *Sphaerotheca breviceps* (Anura) to the common predator *Pantala flavescens* (Odonata). – Salamandra, **59**: 78–82.

Mogali, S. M., B. A. Shanbhag & S. K. Saidapur (2023b): Antipredator responses of *Polypedates maculatus* tadpoles to kairomones from the carnivorous tadpoles of *Hoplobatrachus tigerinus*. – Salamandra, **59**: 83–86.

Mogali, S. M., B. A. Shanbhag & S. K. Saidapur (2023c): Behavioral responses of laboratory-reared and wild-caught *Polypedates maculatus* (Anura: Rhacophoridae) tadpoles to dietary cues from the carnivorous tadpoles of *Hoplobatrachus tigerinus* (Anura: Dicroglossidae). – Phyllomedusa, **22**: 3–10.

Petranka, J. & L. Hayes (1998): Chemically mediated avoidance of a predatory odonate (*Anax junius*) by American toad (*Bufo americanus*) and wood frog (*Rana sylvatica*) tadpoles. – Behavioral Ecology and Sociobiology, **42**: 263–271.

Relyea, R. A. (2007): Getting out alive: how predators affect the decision to metamorphose. – Oecologia, **152**: 389–400.

Scherer, A. E. & D. L. Smee (2016): A review of predator diet effects on prey defensive responses. – Chemoecology, **26**: 83–100.

Schmidt, B. R. & A. Amezquita (2001): Predator-induced behavioral responses: tadpoles of the neotropical frog *Phyllomedusa tarsius* do not respond to all predators. – Herpetological Journal, **11**: 9–15.

Schoeppner, N. M. & R. A. Relyea (2005): Damage, digestion, and defense: the role of alarm cues and kairomones for inducing prey defenses. – Ecology Letters, **8**: 505–512.

Schoeppner, N. M. & R. A. Relyea (2009): When should prey respond to consumed heterospecifics? Testing hypotheses of perceived risk. – Copeia, **2009**: 190–194.

Spieler, M. & K. E. Linsenmair (1999): Aggregation behaviour of *Bufo maculatus* tadpoles as an antipredator mechanism. – Ethology, **105**: 665–686.

Stirling, G. (1995): Daphnia behaviour as a bioassay of fish presence or predation. – Functional Ecology, **9**: 778–784.

Van Buskirk, J. & M. Arioli (2002): Dosage response of an induced defence: how sensitive are tadpoles to predation risk? – Ecology, **83**: 1580–1585.