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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)

Santosh M. Mogali, Bhagyashri A. Shanbhag, and Srinivas K. Saidapur
Karnatak University, Department of Zoology Dharwad-580 003, Karnataka State, India. E-mail: santoshmogali@rediffmail.com.

Abstract
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). The behavioral responses of laboratory-reared and wild-caught tadpoles of *Polypedates maculatus* to predatory tadpoles of *Hoplobatrachus tigerinus* were studied in the laboratory. The predator's diet-derived metabolites released in excreta of predator after consumption of *P. maculatus* tadpoles were used to simulate predation threat. Both laboratory-reared and wild-caught tadpoles of *P. maculatus* showed antipredator behavioral responses i.e., reduced swimming movements and overall time spent in swimming and had a higher burst speed in response to water borne dietary cues of predators. Further, the antipredator responses of wild-caught tadpoles were significantly higher than those exhibited by laboratory-reared tadpoles. The study thus shows that antipredator behavior in these tadpoles is innate. Further, an enhanced antipredator behavior of wild-caught tadpoles may suggest their prior experience with predators in natural waters.

Keywords: Antipredator behavior, Anuran larvae, Dietary cues, Predator-prey interactions.

Resumo
Respostas comportamentais de girinos de *Polypedates maculatus* (Anura: Rhacophoridae) criados em laboratório e capturados na natureza a sinais alimentares dos girinos carnívoros de *Hoplobatrachus tigerinus* (Anura: Dicroglossidae). As respostas comportamentais de girinos de *Polypedates maculatus* criados em laboratório e capturados na natureza aos girinos predadores de *Hoplobatrachus tigerinus* foram estudadas em laboratório. Os metabólitos derivados da dieta do predador liberados na excreta do predador após o consumo de girinos de *P. maculatus* foram usados

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para simular a ameaça de predação. Tanto os girinos de *P. maculatus* criados em laboratório como os capturados na natureza apresentaram respostas comportamentais contra predadores, ou seja, reduziram os movimentos de natação e o tempo total gasto na natação e tiveram uma velocidade de explosão mais alta em resposta a sinais alimentares de predadores na água. Além disso, as respostas anti-predação dos girinos capturados na natureza foram significativamente maiores do que as exibidas pelos girinos criados em laboratório. O estudo mostra, portanto, que o comportamento anti-predação desses girinos é inato. Além disso, um comportamento anti-predação aprimorado dos girinos capturados na natureza pode sugerir sua experiência anterior com predadores em águas naturais.

Palavras-chave: Comportamento anti-predação, Estímulos alimentares, Interações predador-presa, Larvas de anuros.

Introduction

Predation is a chief selection pressure forcing prey organisms to maximize their fitness by recognizing and avoiding predators (Lima and Dill 1990). Consequently, predators can impact behavior, morphology and life history of prey individuals and populations (Lima and Dill 1990, Laforsch and Tollrian 2004). For predator recognition, animals may use cues of different modalities (e.g., visual, acoustic, electric, tactile, chemical) or a combination thereof (Amo *et al.* 2004, McCormick and Manassa 2007, Saidapur *et al.* 2009, Mogali *et al.* 2012, Landeira-Dabarca *et al.* 2019). In aquatic predator-prey systems, chemical signaling is considered particularly relevant, as aquatic chemical cues can usually be detected earlier and over larger distances than visual cues (Chivers *et al.* 1996, Kiesecker *et al.* 1999).

Anuran larvae are an excellent model system for studying predator-prey interactions. Tadpoles are highly vulnerable to aquatic (i.e., fish, insect larvae, other tadpoles etc.) predators (Heyer *et al.* 1975, Gascon 1992, Mogali *et al.* 2020a). Most of the aquatic anuran tadpoles assess predation risk using chemosensory mechanisms to which they respond by means of defensive behaviors (Ferrari *et al.* 2010, Mogali *et al.* 2012, 2020b). Specifically, they perceive alarm cues released by injured prey, kairomones of predators, and dietary cues (excretory metabolites or substances of predators fed conspecific or heterospecific prey) that elicit antipredatory or avoidance behaviors (Brodie *et al.* 1991, Nomura *et al.* 2011, 2013) to escape predation (Wisenden 2000, Schoeppner and Relyea 2005, 2009, Mogali *et al.* 2011, 2012, Scherer and Smee 2016). Earlier studies also revealed that anuran tadpoles showed a variety of antipredatory behaviors to chemical cues of predators; as increased activity or high swimming speed in order to run away from predators (e.g., Mogali *et al.* 2021), reduction in activity (cryptic behavior, e.g., Saidapur *et al.* 2009, Mogali *et al.* 2012), aggregation (e.g., Spieler and Linsenmair 1999), or increased use of refuge sites (e.g., Hossie and Murray 2010, Mogali *et al.* 2019, 2022a).

The Indian tree frog *Polypedates maculatus* (Gray, 1834) is widely distributed in India. It breeds between June-August in South India and females are known to deposit eggs in foam nests attached to vegetation or underneath stones above a water body, or adhered to walls of cement cisterns filled with water and also bushes over the puddles (Mohanty-Hejmadi and Dutta 1988, Girish and Saidapur 1999, Mogali 2018, Mogali *et al.* 2022b). Development occurs inside the foam nests up to Stage 23 of Gosner (1960) after which tadpoles drop into the water to undergo further development and metamorphosis (Mogali 2018). Construction of the foam nest for the protection of eggs and early development of tadpoles is a strategy adopted by *P. maculatus* possibly for avoiding predation during early development (Mogali 2018). During our regular field visits, we have noticed that herbivorous tadpoles of *P. maculatus* are preyed on by carnivorous tadpoles of *Hoplobatrachus tigerinus* (Daudin, 1802) (Saidapur 2001, Saidapur *et al.* 2009, Mogali *et al.* 2020c). Most of the tadpole prey-predator interactions studies focused mainly on aquatic insects, fishes, or salamanders as predators (Chivers and Mirza 2001, Mathis 2003, Mogali *et al.* 2020a,b, 2022a). However, so far, we found few studies showing the effect of carnivorous tadpole predators on the behavioral responses of herbivorous tadpoles. Herein, we studied the behavioral responses of both laboratory-reared (predator-naive) and wild-caught (predator-experienced) *P. maculatus* to the dietary cues of the predator *H. tigerinus*. We hypothesized that dietary cues of predators would elicit avoidance behaviors in both laboratory-reared and wild-caught *P. maculatus* tadpoles. Additionally, we also hypothesized that wild-caught (in which we assume that tadpoles have previously experience with predators) *P. maculatus* tadpoles should display stronger behavioral responses to predators than that of laboratory-reared (no previously experience with predators) tadpoles.

Materials and Methods

Polypedates maculatus *Tadpoles*

Three foam nests of *P. maculatus* were collected in the early monsoon period from temporary ponds in the Karnatak University Campus (15.440407° N, 74.985246° E) Dharwad, Karnataka State, India. Soon after collection they were brought to the laboratory and each nest was placed in separate plastic tubs (32 cm diameter and 14 cm deep) with 1 L of aged tap water along with some substratum collected from the same pond. The tadpoles come out from foam nests almost synchronously after five days at Stage 23 (Gosner 1960). Tadpoles from all three nests were then mixed (50 tadpoles from each nest; 150 tadpoles in total), to avoid bias due to genetic difference among the groups and were reared in a glass aquarium (90 × 30 × 15 cm) containing 20 L of aged tap water. Tadpoles of *H. tigerinus* (stages 31–32, mean total length 36.25 ± 1.04 mm, *N* = 30) and *P. maculatus* (stages 27–28, mean total length 26.40 ± 1.13 mm, *N* = 75) were also collected from the same ponds where the foam nests were collected. Tadpoles of *H. tigerinus* were reared individually in plastic containers (19 cm diameter and 7 cm deep, with 0.5 L of aged tap water) to avoid cannibalism. The wild tadpoles of *P. maculatus* were reared in a glass aquarium (75 × 30 × 15 cm) containing 10 L of aged tap water. The tadpoles of *P. maculatus* are herbivorous (Mogali *et al.* 2022b) hence they were fed with boiled spinach, while the tadpoles of *H. tigerinus* were fed exclusively with *P. maculatus* tadpoles. The tadpoles of *P. maculatus* obtained from foam nests in the laboratory are termed as laboratory-reared tadpoles, whereas wild tadpoles were termed as wild-caught tadpoles. The behavioral responses of the test tadpoles, *P. maculatus* (laboratory-reared and wild-caught) were studied by exposing them to “stimulus solution” of dietary metabolites of predators, *H. tigerinus* fed with conspecific (*P. maculatus*) tadpoles.

Preparation of Dietary Cues of Conspecific Origin

Ten *H. tigerinus* tadpoles were placed in separate plastic tubs (19 cm diameter and 7 cm depth) containing 200 mL of aged tap water along with four tadpoles of *P. maculatus* at stages 27–28 at 08:30 h. In less than 12 hours, all *H. tigerinus* tadpoles have consumed all the *P. maculatus* tadpoles available. On the following day, between 09:30 and 11:30 h, we removed the *H. tigerinus* tadpoles from the tubs and we filtered the water using fine cheesecloth. We used the filtrate as a cue for the water predation risk by *H. tigerinus*, once it contains the diet-derived excretory metabolites from consuming *P. maculatus* tadpoles (Mogali *et al.* 2012, 2020a). Moreover, we considered that the filtrate would not have alarm cues of prey, once these cues were known to be labile in nature (Ferrari *et al.* 2008, Wisenden *et al.* 2009, Chivers *et al.* 2013, Mogali *et al.* 2023).

Experiments

The behavioral responses of laboratory-reared (stages 27–28) and wild-caught (stages 27–28) *P. maculatus* tadpoles to predator's dietary cues were recorded by placing a single *P. maculatus* tadpole in a rectangular glass tank (28 × 15 × 15 cm) containing 600 mL of aged tap water. A handycam (Sony, DCR-SR300/E) was fixed above the tank in a manner that the entire area of the glass tank was visible in the recording. The handycam 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 dietary cues of *H. tigerinus* to the test tank. We recorded the maximum swimming speed (V_{max}), the distance covered by the tadpole, the number of swimming spurts, and the time spent swimming during an entire trial. For each trial, a new tadpole (*P. maculatus*) was first introduced into the tank and left undisturbed for 5 min. The test tank was cleaned and replenished with aged tap water between trials. A burette was placed ~1 cm above the water level and 50 mL of aged tap water (chemical blank) was then added slowly at the rate of ~1 mL/s to simulate the disturbance of the later chemical cue would make. The burette was then removed gently. Movement of the tadpole was then 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 dietary cues of predator was added as described above. Movement of the tadpole was recorded for another 5 min to determine the activity pattern after exposure to dietary cues. We performed 25 trials with laboratory-reared and 25 with wild-caught tadpoles (50 trials in total).

Analyzes

The data size is small and does not attend the normal distribution hence we analyzed the data by applying the non-parametric tests. The behavioral responses of laboratory-reared and wild-caught *P. maculatus* tadpoles, before and after addition of the conditioned water with chemical cues of predator were compared separately using the Wilcoxon paired sign rank test. Behavioral responses exhibited by laboratory-reared and wild-caught tadpoles to conditioned water were compared using the Mann-Whitney U test. Statistical tests were performed using SPSS ver. 16.0.

Results

Tadpoles exposed to dietary cues of *H. tigerinus,* both laboratory-reared and wild-caught, showed a significant increase in the burst speed (V_{max}) but a significant decline in the number of swimming spurts, swimming time, and total distance moved when compared to their baseline activity (Table 1). However, wild-caught tadpoles showed a significant greater burst speed ($U = 4.0$, $p < 0.001$), than that exhibited by laboratory-reared tadpoles similarly exposed to conditioned water. Further, the number of swimming spurts ($U = 114.0$, $p < 0.001$), time spent in swimming ($U = 89.0$, $p < 0.001$), and distance covered ($U = 88.0$, $p < 0.001$) by the wild-caught tadpoles were significantly lower than that exhibited by laboratory-reared tadpoles upon exposure to conditioned water.

Discussion

In natural aquatic systems, anuran tadpoles are at risk of predation, which have drove behavioral response promoting their escape from predators (Schmidt and Amézquita 2001, Relyea 2007). In aquatic systems, various types of chemical cues (e.g., kairomones of predators, alarm cues damaged conspecifics, dietary

Table 1. Behavioral responses of laboratory-reared and wild-caught *Polypedates maculatus* tadpoles in the absence and in the presence of dietary predator cues of *Hoplobatrachus tigerinus,* fed with *P. maculatus* tadpoles. Data are represented as mean ± SE; $N = 25$ trials per treatment; Z = Wilcoxon paired sign rank test, p = Significance level set at 0.01.

Treatment	V_{max} (cm/s)		Swimming spurts		Time spent swimming (s)		Distance traveled (cm)	
	Lab- reared	Wild-caught	Lab- reared	Wild-caught	Lab- reared	Wild-caught	Lab- reared	Wild-caught
Absence of dietary cues	12.27 ± 0.21	12.36 ± 0.22	77.24 ± 2.26	77.80 ± 2.28	69.55 ± 2.45	70.38 ± 2.49	464.78 ± 9.81	466.10 ± 9.90
Presence of dietary cues	20.62 ± 0.32	28.10 ± 0.72	16.92 ±1.01	10.64 ± 0.83	15.14 ± 0.99	8.72 ± 0.74	169.49 ± 7.31	113.83 ± 6.30
Z	-4.372	-4.372	-4.373	-4.373	-4.372	-4.372	-4.371	-4.371
p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

metabolites of predators) affect the behavioral responses of prey (Wisenden 2000, Schoeppner and Relyea 2005, Mogali *et al.* 2011, 2012). Prey often exhibits the strongest behavioral responses when the predator consumes a diet of conspecific prey (Wilson and Lefcort 1993, Schoeppner and Relyea 2005, 2009, Mogali *et al.* 2011).

The results of the present study showed that both laboratory-reared and wild-caught *P. maculatus* tadpoles sensed the dietary cues of predator, *H. tigerinus,* fed with conspecific prey and quickly decreased their activity levels (less time spent in swimming, less distance traversed and few number of swimming spurts) during the trial period. Furthermore, it is interesting to note that whenever the *P. maculatus* tadpoles moved in the stimulus solution (dietary cues) their spurts speed (V_{max}) was higher than in the stimulus blank solution, indicating their efforts to escape from the perceived dietary cues of predator. Our results are in conformity with earlier studies on *Rana temporaria* Linnaeus, 1758 (Laurila *et al.* 1997), *Dryophytes versicolor* (LeConte, 1825) (as *Hyla versicolor* in Schoeppner and Relyea 2009), *Duttaphrynus melanostictus* (Schneider, 1799) (as *Bufo melanostictus* in Mogali *et al.* 2011, 2020a), *Hylarana temporalis* (Günther, 1864) tadpoles (as *Rana temporalis* in Mogali *et al.* 2012) and *Sphaerotheca breviceps* (Schneider, 1799) (Mogali *et al.* 2023). Thus *P. maculatus* tadpoles appear to perceive *H. tigerinus* tadpoles as potential predators. The long ecological co-occurrence of *P. maculatus* tadpoles with sympatric carnivorous tadpoles such as *H. tigerinus* may have led to the evolution of antipredator defense strategies in response to dietary cues of these predators.

The results of the present study also clearly showed that wild-caught tadpoles of *P. maculatus* exhibit enhanced antipredator responses to predator's dietary cues compared to that of laboratory-reared tadpoles. It is likely that wild-caught tadpoles remember their early encounter with predator in the natural waters and hence improve their antipredator responses. Our results are in conformity with earlier studies on tadpoles of *Hylarana temporalis* (as *Rana temporalis* in Mogali *et al.* 2012), *Amerana muscosa* (Camp, 1917) (as *Rana muscosa* in Hammond *et al.* 2023), and the snail *Physa acuta* Draparnaud, 1805 (Turner *et al.* 2006).

In summary, the present study shows that both laboratory-reared and wild-caught *P. maculatus* tadpoles exhibit antipredator behavior to dietary cues of predator fed with conspecific prey items. Further, an enhanced antipredator behavior of wild-caught tadpoles may suggest their prior experience with predators in natural waters.

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