

Predatory Cues Influence the Behavioral Responses and Metamorphic Traits of *Polypedates maculatus* (Anura: Rhacophoridae)

Santosh MOGALI*

Department of Zoology, Karnatak University, Dharwad 580003, India

Abstract Mechanisms of predator detection and the influence of the presence of nonlethal predators on antipredator defense behavior and metamorphic traits were studied in the Indian tree frog, *Polypedates maculatus*. Exposure of *P. maculatus* tadpoles to chemical cues of caged predator (crabs, *Barytelphusa* spp.) fed with either conspecific or heterogeneric tadpoles, or were starved elicited defense behavior (by avoiding predator zone) in them. Such a behavior was not evident when exposed to predators housed in a glass beaker (visual cues). Both early (Gosner stage 27–28) and later (Gosner stage 35–36) stage tadpoles when exposed to caged predators (fed with conspecific tadpoles), prey tadpoles spent less time swimming and remained motionless for longer periods. Yet, the time spent by prey in feeding was unaffected. Further, the predator avoidance behavior exhibited by them was of the same intensity regardless of whether the caged predators were fed or starved implying the influence of predator's kairomones. Tadpoles reared with caged predator reached the metamorphic climax stage (MC stage; Gosner stage 42) earlier than those reared without a predator. Size at emergence (Gosner stage 46) was comparable in both the groups. The findings suggest that *P. maculatus* tadpoles assess predation risk chiefly by sensing kairomones of the predator in eliciting antipredator defense behaviors. Accelerated development and early metamorphosis without any compromise of the size at emergence may be due to their unaltered feeding activity.

Keywords antipredator behavior, *Barytelphusa* spp., chemical cues, visual cues, dietary cues, metamorphosis

1. Introduction

Predation is one of the major causes of tadpole mortality, occurring at all stages of development and metamorphosis (Alford, 1999; Villa *et al.*, 1982) while influencing behavior, morphology, age and size at metamorphosis (Benard, 2004; Laurila *et al.*, 1997; Mogali *et al.*, 2011, 2012, 2015; Saidapur *et al.*, 2009). The aquatic environment where tadpoles live is often turbid or densely vegetated obscuring visual cues and hence most species of tadpoles detect predators through chemical rather than visual cues. Moreover, most tadpoles are nearsighted (Hoff *et al.*, 1999). The source of chemical cues emanating from predators and detected by prey tadpoles

may differ. The chemical cues may arise from the starved predators (kairomones; Mogali *et al.*, 2011; Schoeppner and Relyea, 2005) or metabolites derived following digestion of conspecific or heterospecific prey items and released through feces (Laurila *et al.*, 1997; Mogali *et al.*, 2011). Also, alarm pheromones released by injured prey are reported to serve as a cue to the presence of predators in several species (Chivers and Smith, 1998; Schoeppner and Relyea, 2005). Hence, in aquatic environments most anuran tadpoles respond to chemical cues of predators that were either fed on conspecific or heterospecific or different species of prey (Laurila *et al.*, 1997; Mogali *et al.*, 2011; Schoeppner and Relyea, 2005, 2009).

The Indian tree frog, *Polypedates maculatus* (Gray, 1834; Anura: Rhacophoridae), 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 and bushes over the puddles (Girish and Saidapur, 1999; Mohanty-Hejmadi and Dutta, 1988). Development

* Corresponding author: Dr. Santosh MOGALI, from Department of Zoology, Karnatak University, Dharwad, India, with his research focusing on behavioral ecology of Anuran tadpoles with special reference to prey-predator interactions.
E-mail: santoshmogali@rediffmail.com
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occurs inside the foam nests up to Gosner stage 23 after which tadpoles fall into the water to undergo further development and metamorphosis. Construction of the foam nest for the protection of eggs and early development of the tadpoles is a strategy adopted by *P. maculatus* possibly for avoiding predation during early development (Gosner stage 23). There are no studies on the influence of predator on the behavior of tadpoles and metamorphic traits in species belonging to the family Rhacophoridae. The crabs *Barytelphusa* spp. that co-occur with *P. maculatus* tadpoles in natural water bodies were used as the predator in this study. *Barytelphusa* spp. uses chemoreception in the location of food sources rather than mechanoreceptors and are actively feeding on all stages of *P. maculatus* tadpoles (Personal observation). Therefore, it was of interest to study 1) the mechanism of predator detection; 2) the behavioral responses in tadpoles and; 3) the metamorphic traits (age and size at metamorphosis) of *P. maculatus* exposed to caged predator.

2. Materials and Methods

2.1. Collection and maintenance Three foam nests of *P. maculatus* were sighted in temporary ponds during the peak rainy season (mid-July; 16 July 2015) on the Karnatak University Campus (latitude 15.440407° N, longitude 74.985246° E). The nests were attached to

the vegetation 15–20 cm above the water surface. They were brought to the laboratory and placed in separate plastic tubs (32 cm diameter and 14 cm deep) with 1 L of dechlorinated (aged water) water along with some substratum collected from the same pond. The tadpoles emerged after 5 days from foam nests at Gosner stage 23 (Gosner, 1960). Tadpoles from all three nests were then mixed and reared in tubs (32 cm diameter and 14 cm deep) containing 3 L of water and used for the experiment. The egg masses of the Indian burrowing frog, *Sphaerotheca breviceps*, were also collected from the same locality but a week earlier. After hatching, these tadpoles were reared in plastic tubs (32 cm diameter and 14 cm deep) containing 3 L of water. These were used for feeding predators. From feeding stage (Gosner stage 25), tadpoles of *P. maculatus* and *S. breviceps* were fed with boiled spinach. The crabs (*Barytelphusa* spp.; $n = 50$, used as predators) were collected from the same ponds from where the foam nests and the egg masses were obtained. They were reared individually (to avoid cannibalism) in small plastic tubs (19 cm diameter and 7 cm deep) containing 500 mL of aged tap water. They were fed daily either with tadpoles of *P. maculatus* or *S. breviceps* ($n = 2$).

2.2. Mechanism of predator detection (Experiment 1) This experiment was conducted to better understand whether *P. maculatus* tadpoles detect predators based

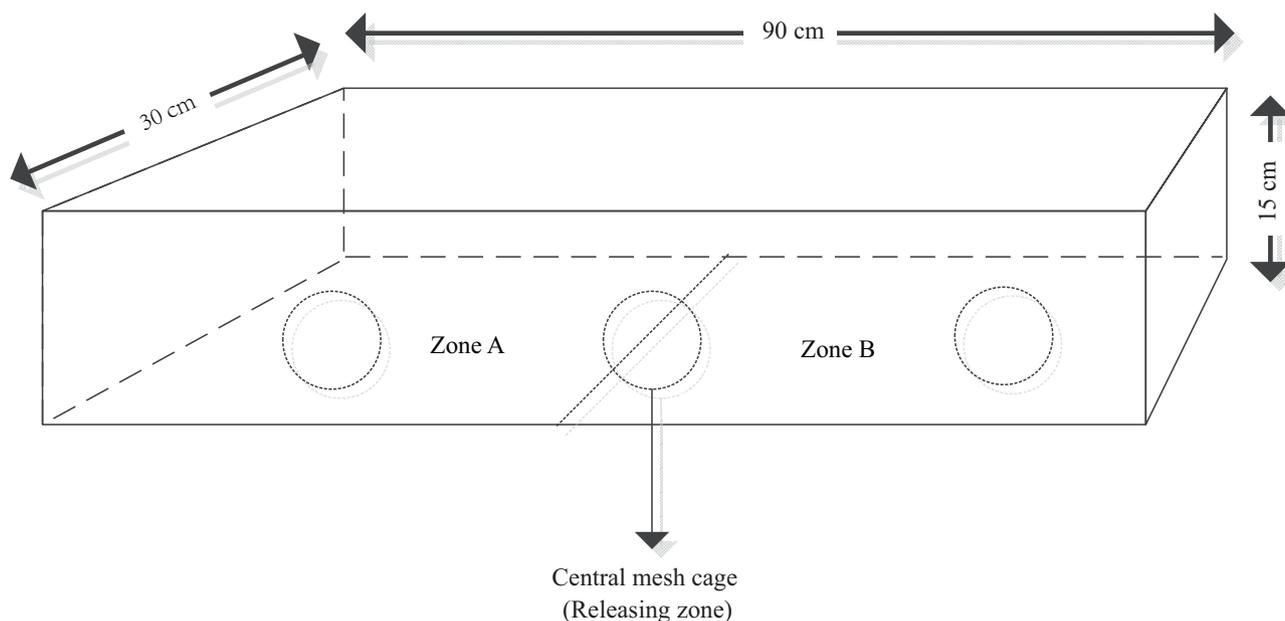


Figure 1 The design of the test apparatus used for determining the mechanism of predator detection by the tadpoles of *Polypedates maculatus*. The dotted central line visually divides the test apparatus into two zones. Circles in the end zones indicate areas where a glass beaker or a mesh cage wrapped with cheese cloth was placed. These containers either housed the predator, *Barytelphusa* spp. (fed with conspecific or heterogeneric tadpoles or starved) or were kept empty.

on chemical or visual cues or both. A rectangular glass apparatus (90 L × 30 W × 15 H cm³) as described in an earlier study (Saidapur *et al.*, 2009) served as the test apparatus (Figure 1). The test apparatus was equally divided into two zones (A and B; Figure 1). For detection of visual cues of predator, one end of the test apparatus was used to house the crab ($n = 1$) in a transparent glass beaker (providing visual cues) and at the opposite end zone of the test apparatus was kept blank. For detection of chemical cues of predator, the one ends of the test apparatus were used to house the crab ($n = 1$) in an open-ended mesh cage (providing chemical cues) and the opposite end was kept blank. Before each trial, the test apparatus was washed and water was renewed to a height of 3 cm. A test tadpole (*P. maculatus*) was placed in the cage (10 cm diameter and 15 cm deep) at the center of the test apparatus and allowed to acclimate as well as perceive predator's chemical/ visual cues for 5 min. The test subject was then released by gently lifting the cage without disturbance. As a measure of predator detection ability of the test tadpole, total time spent by it in each zone (A and B) of the test apparatus was recorded for next 10 min. It is assumed that if test tadpole detects predators it would spend more time in the zone away from the one housing the predators. On the other hand, failure to detect such a threat will result in a random movement of test tadpoles in the test apparatus regardless of the predator's visual/ or chemical cues. The following tests were conducted to record association choice of the tadpoles in response to predatory cues.

End-bias tests These tests were conducted to check whether tadpoles show any bias towards a particular end of the test apparatus. These tests involved three sets of trials, viz. 1) the stimulus zones of the test apparatus without any containers; 2) one stimulus zone with glass beaker containing water to the level that matched the water in the test apparatus and the other zone blank; 3) with a mesh cage wrapped with cheese cloth in one zone and the other zone blank.

Test for detection of visual/ chemical cues of predator

In trials to test the visual acuity for a predator by a tadpole, a predator was placed in a transparent glass beaker at one end of the test apparatus so as to provide visual cues but not their water-borne chemical cues. The opposite end zone of the test apparatus was blank. In trials with chemical cues of predators, a predator was placed in a mesh cage wrapped with cheese cloth at one end of the test apparatus that provided chemical but not visual cues to the test subjects. Three sets of trials were

conducted in this test. In the first set, a predator fed on *P. maculatus* (conspecific) tadpoles, in the second set, a predator fed on *S. breviceps* (heterogeneric) tadpoles and in the third set of trials, a predator which was starved for 24 h (kairomones; do not contain any diet derived metabolites) was placed in a mesh cage wrapped with cheese cloth at one end of the test apparatus that provided its chemical but not visual cues to the test subjects. The opposite end zone of the test apparatus was blank. Each test comprised of 20 trials with new tadpoles each time. The test apparatus was washed after every trial. Data on the time spent by test tadpoles in stimulus zones A and B were compared by the Wilcoxon matched-pairs signed-ranks test.

2.3. Influence of predatory cues on the behavior of tadpoles (Experiment 2)

In this experiment, predators fed with conspecific tadpoles were used to study the behavioral responses in *P. maculatus* tadpoles. The experiments were conducted using Gosner stage 27–28 (early stage) and Gosner stage 35–36 (later stage) tadpoles.

Polypedates maculatus tadpoles ($n = 10$; Gosner stage 23) were reared in plastic tubs (32 cm diameter and 14 cm deep) with 3 L of aged tap water. A small tub (19 cm diameter and 7 cm deep) with perforations (1.2 mm² holes) and wrapped with nylon mesh was placed in the center of the rearing tub either kept empty (group-I; control) or housed the predator fed on conspecific tadpoles (group-II).

Each group consisted of five replicates. The prey tadpoles were fed with boiled spinach *ad libitum*. An individual tadpole from each group was chosen at a time as focal animal and was observed for 30 min. As a measure of antipredator defense behavior, time spent in swimming or feeding or remaining motionless (stationary phase) by the focal individual was recorded. The trials were conducted on alternate days following replenishment of food and water. Twenty trials were conducted for each group of tadpoles in early (Gosner stage 27–28) and later stages (Gosner stage 35–36). In total 80 trials were conducted (i.e. 40 trials for early; for each group 20 trials and 40 trials for later stages tadpoles; for each group 20 trials). The data on time spent in swimming, feeding and stationary phase between two groups were analyzed by Mann-Whitney *U* test.

2.4. Influence of caged predator on metamorphic traits (Experiment 3)

In this, as in experiment 2, the tadpoles were reared in tubs with or without caged predator until MC stage (Gosner stage 42; emergence of forelimbs). The

date of reaching MC for each individual was recorded. On reaching MC, tadpoles were kept in small plastic tubs (19 cm diameter and 7 cm deep) with little water covered with fine nylon mesh and kept inclined to provide a semi-terrestrial area to facilitate emergence. At metamorphosis, snout-vent length (SVL, in mm) and body mass (in mg) were recorded. One tadpole in group-II died during the course of the experiment. Data on SVL, body mass and time taken to reach MC between two groups were analyzed by Mann-Whitney U test.

3. Results

3.1. Mechanism of predator detection (Experiment 1)

In the end-bias tests, tadpoles moved freely throughout the test tank. They showed no bias towards any particular side of the test apparatus or glass beaker or mesh cage. Hence, data from all sets of end-bias tests were pooled and are presented in Table 1 ($Z = -1.100$, $P = 0.912$). In trials with visual cues of predators at one end zone, the test tadpoles moved randomly and freely throughout the test arena. The time spent by prey tadpoles near or away from the predators was comparable ($Z = -4.480$, $P = 0.654$; Table 1). In trials with water-borne chemical cues of predators (fed on conspecific tadpoles), the test tadpoles spent the significantly greater amount of time away from them ($Z = -3.136$, $P < 0.002$; Table 1). Likewise, in trials with chemical cues of predators fed on heterogeneric tadpoles ($Z = -2.987$, $P < 0.003$; Table 1) or starved predator ($Z = -2.502$, $P < 0.020$; Table 1), the prey tadpoles spent the significantly greater amount of

time away from the predator zone.

3.2. Influence of predatory cues on the behavior of tadpoles (Experiment 2)

Tadpoles of *P. maculatus* (both early and later stages), when exposed to a predator fed with conspecific prey items swam for a significantly short period compared to the control group (early stages: $U = 75.0$, $P < 0.001$, Figure 2A; later stages: $U = 108.0$, $P < 0.020$, Figure 3A). Also, they remained motionless for significantly longer periods (early stages: $U = 67.500$, $P < 0.001$, Figure 2B; later stages: $U = 119.0$, $P < 0.030$, Figure 3B) compared to the control group. However, time spent in feeding was comparable in both the groups (early stages: $U = 165.0$, $P = 0.355$, Figure 2C; later stages: $U = 186.500$, $P = 0.718$, Figure 3C).

3.3. Influence of caged predator on metamorphic traits (Experiment 3)

Tadpoles of *P. maculatus* reared in presence of predator fed with conspecific prey reached MC earlier than the control group ($U = 709.0$, $P < 0.001$; Table 2). However, size (SVL and body mass) at metamorphosis was comparable in both the groups (SVL: $U = 1210.0$, $P = 0.916$, Table 2; body mass: $U = 1200.0$, $P = 0.864$, Table 2).

4. Discussion

In the present study, tadpoles of *P. maculatus* do not detect predator by visual cues as evident from their free movement in the areas housing predator in a glass beaker as reported in earlier studies (Mogali *et al.*, 2012; Saidapur *et al.*, 2009; Stauffer and Semlitsch, 1993). The

Table 1 Association choice of *Polypedates maculatus* tadpoles in response to visual/ chemical stimuli from a predator, *Barytelphusa* spp. ($n = 20$ trials per test).

Test	Mean time (s) spent \pm SE		$Z^{\#}$ and P values
	Zone A	Zone B	
End-bias	302.83 \pm 14.74	297.17 \pm 14.74	$Z = -1.100$, $P = 0.912$
Blank (A) vs. visual (B)	284.75 \pm 29.55	315.25 \pm 29.55	$Z = -4.480$, $P = 0.654$
Blank (A) vs. conspecific tadpole-fed predator (B)	381.45 \pm 19.30	218.55 \pm 19.30	$Z = -3.136$, $P < 0.002^*$
Blank (A) vs. heterogeneric tadpole-fed predator (B)	377.20 \pm 21.01	222.80 \pm 21.01	$Z = -2.987$, $P < 0.003^*$
Blank (A) vs. starved predator (B)	371.80 \pm 24.03	228.20 \pm 24.03	$Z = -2.502$, $P < 0.020^*$

$^{\#}$ Wilcoxon matched-pairs signed-ranks test; * indicates significant difference.

Table 2 Effect of caged predator fed on conspecific tadpoles on metamorphic traits of *Polypedates maculatus*.

Groups	Metamorphic traits (mean \pm SE)		
	SVL (mm)	Body mass (mg)	Days to reach Metamorphic climax
I. Prey tadpoles (control) ($n = 50$)	17.39 \pm 0.09	464.76 \pm 7.16	74.62 \pm 0.72
II. Prey tadpoles + caged predator fed on conspecific tadpoles ($n = 49$)	17.37 \pm 0.09	461.43 \pm 6.84	70.71 \pm 0.55
$U^{\#}$ and P values	$U = 1210.0$, $P = 0.916$	$U = 1200.0$, $P = 0.864$	$U = 709.0$, $P < 0.001^*$

$^{\#}$ Mann-Whitney U test, $n =$ number of tadpoles, * indicates significant difference between the two groups.

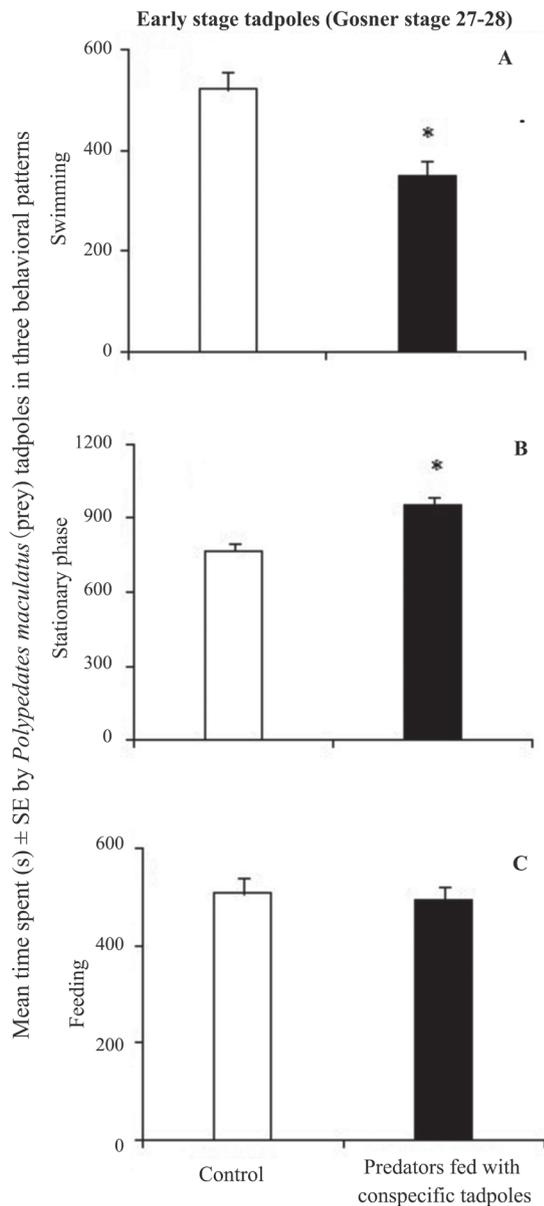


Figure 2 Mean time spent (s) in swimming (A), stationary phase (B), and feeding (C) by the early stage tadpoles (*Polypedates maculatus*) exposed to either chemical cues of caged predators fed with conspecific (prey) tadpoles or without predators (control). Asterisks over the bars indicate significant difference between the two groups (Mann-Whitney *U* test) ($n = 20$ trials per group).

detection of predators by chemical cues is reported in several species of tadpoles (Kiesecker *et al.*, 1996; Mogali *et al.*, 2012; Saidapur *et al.*, 2009; Stauffer and Semlitsch, 1993). A few species are known to detect the predator using its kairomones (Mogali *et al.*, 2011; Schoeppner and Relyea, 2005) while others detect based on the dietary cues arising from the faecal matter of conspecific prey consuming predators (Laurila *et al.*, 1997; Mogali *et al.*, 2011, 2012), and yet others detect the predator by alarm cues released following injury of conspecifics (Chivers

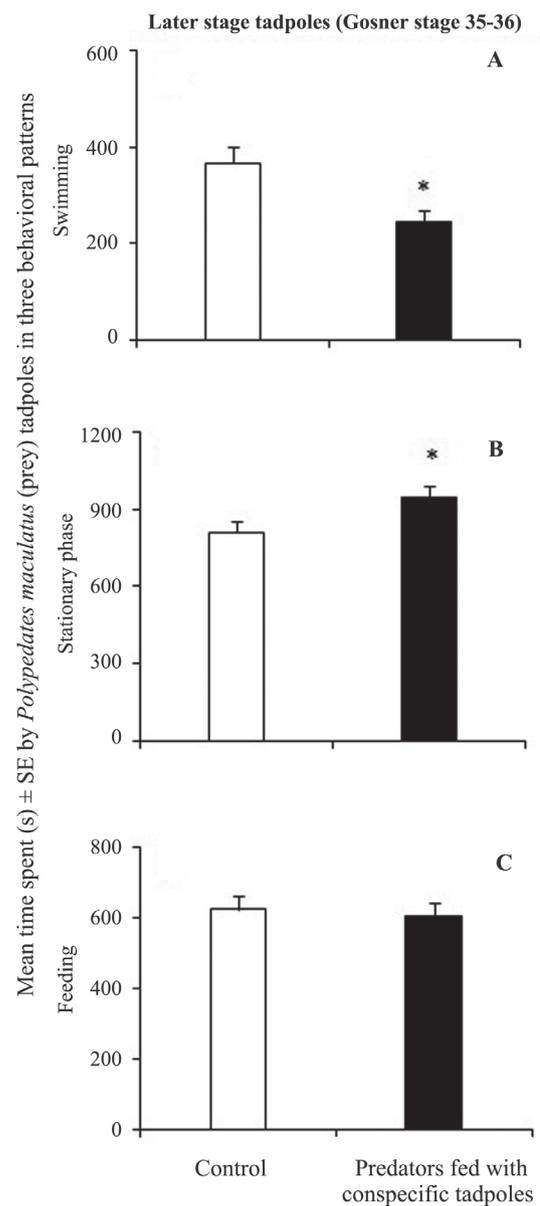


Figure 3 Mean time spent (s) in swimming (A), stationary phase (B), and feeding (C) by the later stage tadpoles (*Polypedates maculatus*) exposed to either chemical cues of caged predators fed with conspecific (prey) tadpoles or without predators (control). Asterisks over the bars indicate significant difference between the two groups (Mann-Whitney *U* test) ($n = 20$ trials per group).

and Smith, 1998; Mogali *et al.*, 2011; Schoeppner and Relyea, 2005). However, they detect predators using kairomones released by the predator regardless of whether they are starved or fed with conspecific or heterogeneric tadpoles.

In the present study, results of experiment 2 showed that when *P. maculatus* tadpoles exposed to predators fed with conspecific tadpoles spent less time in swimming and remaining motionless for longer time than those tadpoles exposed without predators (control). Also, the

antipredator behavior measured in terms of time spent in the zone housing predator (experiment 1) showed that the tadpoles of *P. maculatus* exhibit more or less identical responses to a predator that was starved or fed with either conspecific or heterogeneric tadpoles. Tadpoles of tree frog, *Hyla versicolor* are also reported to exhibit an identical response to predator regardless of whether fed with tadpoles of conspecific or other amphibian species (Schoeppner and Relyea, 2009). The tadpoles of *B. melanostictus* exhibit antipredatory behavior when exposed to a starved predator, but their responses were more intense when exposed to predator fed on conspecific prey suggesting a combined additive response for kairomones and chemical cues of dietary origin following consumption of conspecific prey items (Mogali *et al.*, 2011). Since the intensity of antipredator responses of *P. maculatus* tadpoles is similar regardless of whether exposed to starve or fed predator, it appears that they mainly respond to kairomones arising from the predator.

Earlier studies have shown that the presence of predators can influence the metamorphic traits in different ways (Lardner, 2000; Mogali *et al.*, 2011, 2016; Relyea, 2007; Vonesh and Warkentin, 2006). *Rana temporaria* metamorphose late and emerge at a larger size under the influence of predatory cues (Laurila *et al.*, 1998; Nicieza, 2000). In contrast, *Hylarana (Rana) temporalis* metamorphose early and also at a larger size (Mogali *et al.*, 2016). On the other hand *Bufo bufo*, *Rana aurora* that metamorphose early in presence of predator invariably emerged at a smaller size (Kiesecker *et al.*, 2002; Lardner, 2000). A few others metamorphose at a smaller size without any change in the larval period (Lardner, 2000). Some others metamorphose late and emerge with a larger or same (Relyea, 2007) or at a smaller size (Mogali *et al.*, 2011). The diversity in the trade-off between size at metamorphosis and larval period appears to depend upon ecological conditions where the tadpoles dwell, type of predator (ambush or active), and the energy spent on antipredator behavior and foraging. An earlier study on *B. melanostictus* correlated feeding time and antipredator behavior to metamorphic traits. In the presence of a predator, tadpoles of *B. melanostictus* fed for a shorter period and metamorphosed late at a smaller size (Mogali *et al.*, 2011). In the present study, *P. maculatus* metamorphosed early and yet the size at metamorphosis was unaffected. Unlike in *B. melanostictus*, *P. maculatus* tadpoles fed well and at the same time, energy was conserved by reducing their swimming activity. Therefore, the size of metamorphs was not affected despite rearing with caged predators.

In summary, tadpoles of *P. maculatus* perceive predation risk by detecting kairomones emanating from the predator and emerge earlier than those reared in the absence of the predator. But the size of metamorphs was unaffected unlike in some other species that metamorphose earlier in presence of predator at a smaller size or at a larger size. They accomplish this by staying in stationary phase for a longer time with less swimming activity and avoiding the zone inhabited by the predator.

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References

- Alford R. A. 1999. Ecology, resource use and predation. In: McDiarmid RW, Altig R (eds) Tadpoles: the biology of anuran larvae. The University of Chicago Press, Chicago, pp 240–278
- Benard M. F. 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. *Annu Rev Ecol Evol Syst*, 35: 651–673
- Chivers D. P., Smith R. J. F. 1998. Chemical alarm signaling in aquatic predator-prey systems: a review and prospectus. *Ecoscience*, 5: 338–352
- Girish S., Saidapur S. K. 1999. Mating and nesting behavior, and early development in the tree frog *Polypedates maculatus*. *Curr Sci*, 76: 91–92
- Gosner K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16: 183–190
- Hoff K. V. S., Blaustein A. R., McDiarmid R. W., Altig R. 1999. Behaviour: interaction and their consequences. In Tadpoles: Biology of anurans larvae (eds McDiarmid RW and Altig R) University of Chicago Press, Chicago, pp 215–239
- Kiesecker J. M., Chivers D. P., Blaustein A. R. 1996. The use of chemical cues in predator recognition by Western toad tadpoles. *Anim Behav*, 52: 1237–1245
- Kiesecker J. M., Chivers D. P., Anderson M., Blaustein A. R. 2002. Effect of predator diet on the life history shifts of Red-legged frogs, *Rana aurora*. *J Chem Ecol*, 28: 1007–1015
- Lardner B. 2000. Morphological and life history responses to predators in larvae of seven anurans. *Oikos*, 88: 169–180
- Laurila A., Kujasalo J., Ranta E. 1997. Different antipredator behavior in two anuran tadpoles: effect of predator diet. *Behav Ecol Sociobiol*, 40: 329–336
- Laurila A., Kujasalo J., Ranta E. 1998. Predator-induced changes in life history in two anuran tadpoles: effects of predator diet.

- Oikos, 83: 307–317
- Mogali S. M., Saidapur S. K., Shanbhag B. A.** 2011. Levels of predation modulate antipredator defense behavior and metamorphic traits in the toad *Bufo melanostictus*. *J Herpetol*, 45: 428–431
- Mogali S. M., Saidapur S. K., Shanbhag B. A.** 2012. Tadpoles of the bronze frog (*Rana temporalis*) assess predation risk before evoking antipredator defense behavior. *J Ethol*, 30: 379–386
- Mogali S. M., Shanbhag B. A., Saidapur S. K.** 2015. Strong food odors mask predation risk and affect evocation of defense behaviors in the tadpoles of *Sphaerotheca breviceps*. *J Ethol*, 33: 41–46
- Mogali S. M., Saidapur S. K., Shanbhag B. A.** 2016. Influence of desiccation, predatory cues, and density on metamorphic traits of the bronze frog *Hylarana temporalis*. *Amphibia–Reptilia*, 37: 199–205
- Mohanty-Hejmadi P., Dutta S. K.** 1988. Life history of the common Indian tree frog, *Polypedates maculatus* (Gray, 1834) (Anura: Rhacophoridae). *J Bombay Nat Hist Soc*, 85: 512–517
- Nicieza A. G.** 2000. Interacting effects of predation risk and food availability on larval anuran behavior and development. *Oecologia*, 123: 497–505
- Relyea R. A.** 2007. Getting out alive: how predators affect the decision to metamorphose. *Oecologia*, 152: 389–400
- Saidapur S. K., Veeranagoudar D. K., Hiragond N. C., Shanbhag B. A.** 2009. Mechanism of predator-prey detection and behavioral responses in some anuran tadpoles. *Chemoecology*, 19: 21–28
- Schoeppner N. M., Relyea R. A.** 2005. Damage, digestion, and defense: the roles of alarm cues and kairomones for inducing prey defenses. *Ecol Lett*, 8: 505–512
- Schoeppner N. M., Relyea R. A.** 2009. When should prey respond to consumed heterospecifics? Testing hypotheses of perceived risk. *Copeia*, 2009: 190–194
- Stauffer H., Semlitsch R. D.** 1993. Effects of visual, chemical and tactile cues of fish on the behavioral responses of tadpoles. *Anim Behav*, 46: 355–364
- Villa J., McDiarmid R. W., Gallardo J. M.** 1982. Arthropod predators of Leptodactylidae frog foam nests. *Brenesia*, 19: 577–589
- Vonesh J. R., Warkentin K. M.** 2006. Opposite shifts in size at metamorphosis in response to larval and metamorph predators. *Ecology*, 87: 556–562