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Relative susceptibility of tadpoles of *Uperodon taprobanicus* (Anura: Microhylidae) and *Duttaphrynus melanostictus* (Anura: Bufonidae) to predacious *Hoplobatrachus tigerinus* (Anura: Dicroglossidae) tadpoles: significance of refugia and swimming speed in predator avoidance

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Abstract
Relative susceptibility of tadpoles of *Uperodon taprobanicus* (Anura: Microhylidae) and *Duttaphrynus melanostictus* (Anura: Bufonidae) to predacious *Hoplobatrachus tigerinus* (Anura: Dicroglossidae) tadpoles: significance of refugia and swimming speed in predator avoidance. The relative susceptibility of two closely associated herbivorous tadpole species (*Uperodon taprobanicus* and *Duttaphrynus melanostictus*) to their natural carnivorous predatory tadpole, *Hoplobatrachus tigerinus* and the significance of refugia in predator avoidance was studied in the laboratory. In a total of 50 trials, 10 tadpoles each of *U. taprobanicus* and *D. melanostictus* of comparable sizes were exposed to starved *H. tigerinus*. Twenty-five trials included refugia while 25 did not. The results of this study showed that in both the presence and absence of refugia, *D. melanostictus* tadpoles fell prey to *H. tigerinus* more frequently than *U. taprobanicus* tadpoles. A key difference between the two prey species is the speed of swimming; V_{max} of *D. melanostictus* (13.58 cm/s) tadpoles is significantly lower than that of *U. taprobanicus* (24.89 cm/s) tadpoles. This is likely to be the main reason why more *D. melanostictus* tadpoles were preyed upon than were *U. taprobanicus* tadpoles. It is important to note that the V_{max} of the predator (60.21 cm/s) is much greater than those of the two prey species. However, predation risk of both prey tadpole species was affected significantly by the presence of refugia. The susceptibility of both prey tadpole species was lower where refugia were available. The present study clearly demonstrates that the more efficient avoidance of predation by *U. taprobanicus* tadpoles could be due to better use of refugia and their faster rate of movement.

Keywords: Antipredator behavior, Anuran larvae, Ephemeral ponds, Mortality, Predation threat, Prey-predator interactions, Refuge use.

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Resumo

Suscetibilidade relativa dos girinos de *Uperodon taprobanicus* (Anura: Microhylidae) e *Duttaphrynus melanostictus* (Anura: Bufonidae) aos girinos predadores de *Hoplobatrachus tigerinus* (Anura: Dicroglossidae): importância dos refúgios e da velocidade de natação para evitar o predador. A suscetibilidade relativa de duas espécies de girinos herbívoros intimamente associados (*Uperodon taprobanicus* e *Duttaphrynus melanostictus*) ao seu girino predador carnívoro natural, *Hoplobatrachus tigerinus,* e a importância do refúgio na fuga do predador foram estudadas em laboratório. Em um total de 50 testes, 10 girinos de *U. taprobanicus* e 10 girinos de *D. melanostictus* de tamanhos comparáveis foram expostos a girinos de *H. tigerinus* famintos. Vinte e cinco testes incluíram refúgios, enquanto 25 não incluíram. Os resultados desse estudo mostraram que, tanto na presença como na ausência de refúgios, os girinos de *D. melanostictus* foram predados com mais frequência do que os girinos de *U. taprobanicus.* Uma diferença importante entre as duas espécies de presas é a velocidade de natação; a *Vmax* dos girinos de *D. melanostictus* (13,58 cm/s) é significativamente menor do que a dos girinos de *U. taprobanicus* (24,89 cm/s). É provável que esse seja o principal motivo pelo qual mais girinos de *D. melanostictus* foram predados em relação aos girinos de *U. taprobanicus.* É importante observar que a *Vmax* do predador (60,21 cm/s), é muito maior do que a das duas espécies de presas. No entanto, o risco de predação de ambas as espécies de girinos foi afetado significativamente pela presença de refúgios. A suscetibilidade de ambas as espécies de girinos foi menor quando havia refúgios disponíveis. O presente estudo demonstra claramente que a evasão mais eficiente da predação pelos girinos de *U. taprobanicus* pode ser devida ao melhor uso dos refúgios e à sua taxa de movimento mais rápida.

Palavras-chave: Ameaça de predação, Comportamento anti-predador, Girinos, Interações predador-presa, Lagoas temporárias, Mortalidade, Uso de abrigos.

Introduction

The interaction between predator and prey is an evolutionary arms race in which early detection by either party is often the key to their success (Ferrari *et al.* 2010). Predation leads certainly to the elimination of prey individuals from an ecological system, which can have major impacts on the population dynamics of prey organisms. Therefore, for any prey organism it is important to assess predation risk accurately and develop necessary antipredator defense strategies in order to optimize its survival and fitness (Lima and Dill 1990). Most of the anurans opportunistically breed in temporary water bodies and their larvae live in such waters until metamorphosis (Newman 1992, Saidapur 2001). In such aquatic systems, larval anurans commonly face threats from pond desiccation, crowding, limited food resources, and more importantly from predators. As a consequence, they have evolved a variety of defense strategies (Loman 1999, Lardner 2000, Benard 2004, Mogali *et al.* 2011, 2017). The most common antipredator defense strategies of anuran tadpoles observed to perceived predation threat include increased activity or high swimming speed in order to run away from predators (Hews 1988, Van Buskirk and McCollum 2000), reduction in activity levels to avoid detection or also reduce the encounter rate with predators, especially ambush predators (Schmidt and Amezquita 2001, Saidapur *et al.* 2009, Mogali *et al.* 2011, Hossie *et al.* 2017), aggregation (Spieler and Linsenmair 1999) and increased use of refuge sites (Hossie and Murray 2010, 2011, Mogali *et al.* 2019, 2022) depending upon species. Because they exist in aquatic environments, anuran larvae mostly use chemical signals to assess predation threats since visual information may be obscured in water that is turbid or densely vegetated (Kiesecker *et al.* 1996, Mogali 2018).

In and around the city of Dharwad, Karnataka state of Southern India, many anuran species including the present study species, the Asian common toad, *Duttaphrynus melanostictus* (Schneider, 1799) (family: Bufonidae) and the Indian painted frog, *Uperodon taprobanicus* (Parker 1934) (family: Microhylidae) reproduce in rain-filled ephemeral water bodies formed during the South-West monsoon (Saidapur 2001, Mogali *et al.* 2017). The tadpoles of *D. melanostictus* and *U. taprobanicus* are mainly bottom dwellers and thrive on detritus and algal matter. The visibility is generally low in these ephemeral water bodies due to shadows from vegetation, turbid water and the benthic area that is naturally covered by leaf litter and detritus (our personal observation). These water bodies are also home to several types of invertebrate and vertebrate predators, including the carnivorous tadpoles of the Indian bullfrog, *Hoplobatrachus tigerinus* (Daudin, 1802) (family: Dicroglossidae). The tadpoles of *H. tigerinus* are voracious predators that hunt actively and detect their prey including tadpoles by means of both visual and chemical senses. All three study species used in the present experiment have conservation status Least Concern according to the IUCN Red List (Van Dijk *et al.* 2004, Padhye *et al.* 2008, Inger *et al.* 2016). During our regular field visits, we noticed that herbivorous tadpoles of *D. melanostictus* and *U. taprobanicus* are preyed upon by carnivorous tadpoles of *H. tigerinus.* Most studies of the tadpole prey-predator interactions studies have focused mainly on aquatic insects, fishes, or salamanders as predators (e.g., Chivers and Mirza 2001, Mathis 2003, Mogali *et al.* 2020). So far there seems to be a paucity of research showing the influence of carnivorous tadpoles on the behavioral responses of herbivorous tadpoles.

In natural environments, we noticed many similarities between tadpoles of *D. melanostictus* and *U. taprobanicus*. Hence, it is very important to know about the relative susceptibility of tadpoles to their common predator, *H. tigerinus.* The present study was designed to determine the relative susceptibility of wild-caught tadpoles of *D. melanostictus* and *U. taprobanicus* of comparable body size at early stages of development (Gosner stages 26–27) to the free moving active predator, *H. tigerinus,* both in the presence and the absence of refuge sites. In the present study, we primarily hypothesized that the presence of refuge sites (leaf-litter) could reduce the vulnerability of both species and we secondarily hypothesized that there should be a difference in vulnerability between two prey tadpole species. Thus, the outcome of this study will provide some novel information in the field of behavioral ecology of anuran tadpoles with special reference to prey-predator interactions.

Materials and Methods

Tadpoles of *Uperodon taprobanicus* (Gosner stages 26–27; *N* = ~600; Gosner 1960) and *Duttaphrynus melanostictus* (Gosner stages 26–27; *N* = ~600) were collected from temporary ponds in and around (within 0.5 km distance) the Karnatak University Campus (latitude 15.440407° N, longitude 74.985246° E, elevation 750 m a.s.l.), Dharwad, Karnataka state, India. Soon after collection, they were brought to the laboratory. Tadpoles of each species were placed separately in glass aquaria (90 × 30 × 15 cm) containing 25 L of aged tap water and used as a stock. Tadpoles of both species are herbivores and were fed boiled spinach to sustain growth and development. The tadpoles of *Hoplobatrachus tigerinus* (Gosner stages 32–33; *N* = ~80; predators) were also collected from the temporary ponds in the Karnatak University campus. They were reared individually in plastic tubs (14 cm diameter and 7 cm deep) with 500 mL of aged tap water to avoid cannibalism. Prior to the commencement of the experiment, each predator tadpole was fed daily equally with both prey species (3 *U. taprobanicus* + 3 *D. melanostictus* tadpoles; Gosner stages 26–27) for at least three days.

Experiment 1: Relative Susceptibility of Prey Species

This experiment was designed to determine the relative susceptibility of *U. taprobanicus* and *D. melanostictus* tadpoles to the predator *H. tigerinus* and the significance of refugia in predator avoidance. We carried out a total of fifty experimental trials in a five day period. Ten trials were conducted per day, in ten separate experimental tubs each containing one of two treatments. Each trial started at 7:00 am and ended at 7:00 am the next day. In each trial, ten tadpoles each of *U. taprobanicus* (Gosner stages 26–27; 16.30 ± 0.25 mm in total length; mean ± SE; *N* = 100) and *D. melanostictus* (Gosner stages 26–27; 16.32 ± 0.28 mm in total length; mean ± SE; *N* = 100) of comparable body sizes were released in a plastic tub (32 cm diameter and 14 cm deep) containing 3 L of aged tap water. They were allowed to acclimate for 30 min. Then one *H. tigerinus* tadpole (Gosner stages 32–33; 37.45 ± 0.35 mm in total length; mean ± SE; *N* = 25) starved for 48 h was introduced into the tub. After 24 h the number of surviving *U. taprobanicus* and *D. melanostictus* tadpoles was recorded to compute the number of tadpoles of each species lost due to predation.

In twenty-five trials (five per day over five days) the tubs containing the tadpoles and predators provided no refugia for the prey tadpoles. In a second twenty-five trials, carried out five per day over the same five days, the tubs contained structural refugia made using water soaked (2 days) leaves of *Eucalyptus* (dry mass 15 ± 0.4 g; mean ± SE) chopped into ~1 cm^2 pieces. These were spread at the bottom of the testing tubs to serve as shelters. Predation risk was studied as described above. The experimental tubs in all trials were cleaned before each trial. The experimental tubs were placed on a flat surface in a room temperature (25°C). The positions of the experimental tubs were randomized daily to avoid possible effects of position. The daily water temperature of various tubs (with refugia and without refugia) fluctuated between 23–24°C. All experimental trials were carried out under natural photoperiod (12 h light: 12 h dark). Both prey tadpole species were well fed with boiled spinach before the experimental trials. However, during the trial period they were not provided any food. All test tadpoles used in the experiment were healthy. Data were analyzed using mixed model ANOVA where the effects of experimental containers were included as random effects, and the effects of prey species identity and refuge access and their interaction were included as fixed effects. Relative susceptibility of *U. taprobanicus* and *D. melanostictus* tadpoles to predation in each experiment was tested using Independent samples t test (SPSS software ver. 16.0).

Experiment 2: Burst Swimming Speed of Prey and Predator Tadpoles

Experiment 1 showed that susceptibility of the prey species (*D. melanostictus* and *U. taprobanicus* tadpoles) to predation by *H. tigerinus* tadpoles differed significantly. Hence, it was of interest to know the differences in the swimming speeds of prey species and also the predator species. To determine V_{max}, a single test tadpole of one of the three species (either prey, *D. melanostictus* or *U. taprobanicus* or predator, *H. tigerinus*) was placed in a plastic tub (20 cm diameter and 10 cm deep) filled with aged tap water to a depth of 2.5 cm and left undisturbed for 5 min to adjust to new conditions. A handycam (Sony, DCR-SR300/E) was positioned above the plastic tub to record activity in the entire tub. The handycam was connected to a computer with the Ethovision Video Tracking System (Noldus Information Technology, The Netherlands) to track the movements of the test tadpole. After 5 min of acclimation, the test tadpole was chased continuously for 1 min by prodding the tail base with a delicate wire as described by Van Buskirk and McCollum (2000). The movement of the tadpole was tracked to determine the V_{max}. A total of 25 trials were carried out for each tadpole species with a new healthy test tadpole of each species every time. All test tadpole were well fed before trials. The obtained V_{max} of tadpole species were compared by one-way ANOVA followed by Tukey HSD post-hoc test (SPSS software ver. 16.0).

Results

Experiment 1: Relative Susceptibility of Prey Species

Mixed model ANOVA showed significant main effect of species ($p < 0.01$, Table 1) and refuge availability ($p < 0.01$, Table 1) but not of their interaction ($p = 0.268$, Table 1).

Both in the absence ($t_{48} = -11.415$, $p < 0.01$) and presence ($t_{48} = -10.415$, $p < 0.01$) of refugia significantly more *D. melanostictus* than *U. taprobanicus* tadpoles fell prey to *H. tigerinus* tadpoles (Table 2). Predation threat to tadpoles of both species was affected significantly by the presence of refugia. The susceptibility of both tadpole species (*U. taprobanicus*: $t_{48} = 7.250$, $p < 0.01$; *D. melanostictus*: $t_{48} = 7.071$, $p < 0.01$) to predation was low where refugia were available (Table 2).

Experiment 2: Burst Swimming Speed of Prey and Predator Tadpoles

There was a significant difference in the swimming speed among tadpole species ($F_{2, 72} = 4243.0$, $p < 0.01$; Figure 1). The predacious *H. tigerinus* tadpoles exhibited a significantly greater ($p < 0.01$) V_{max} (60.21 cm/s; Figure 1) than the prey tadpole species. The *U. taprobanicus* tadpoles exhibited a significantly higher ($p < 0.01$) V_{max} (24.89 cm/s; Figure 1) than that of *D. melanostictus* tadpoles (13.58 cm/s; Figure 1).

Table 1. Results of mixed model ANOVA for species and refuge sites and their interactions. The response variable is the mean number of prey tadpoles (*Uperodon taprobanicus* and *Duttaphrynus melanostictus*) lost due to predation by *Hoplobatrachus tigerinus* tadpoles. *Indicates significant differences.

Source	*df*	MS	*F*	*p*
Species	1	94.090	238.706	< 0.01*
Refuge sites	1	39.090	100.693	< 0.01*
Species × refuge sites	1	0.490	1.243	0.268

Table 2. Number of prey tadpoles (mean ± SE) of *Uperodon taprobanicus* (Gosner stages 26–27) and *Duttaphrynus melanostictus* (Gosner stages 26–27) consumed by the predator, *Hoplobatrachus tigerinus* (Gosner stages 32–33) in a 24 h trial period (*N* = 25 trials per treatment). #Independent samples t test; *indicates significant difference between two treatments.

Treatment	Tadpoles consumed		*t* and *p* values#
	U. taprobanicus	*D. melanostictus*	
Without refuge sites	2.76 ± 0.11	4.84 ± 0.15	$t_{48} = -11.415$, $p < 0.01$*
With refuge sites	1.64 ± 0.12	3.44 ± 0.13	$t_{48} = -10.415$, $p < 0.01$*
t and *p* values#	$t_{48} = 7.250$, $p < 0.01$*	$t_{48} = 7.071$, $p < 0.01$*	

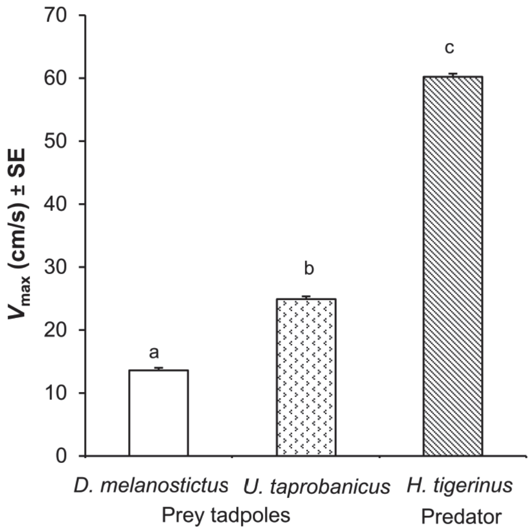

Figure 1. Shows burst swimming speed (V_{max}) of prey (*Duttaphrynus melanostictus*, *Uperodon taprobanicus*) and predator (*Hoplobatrachus tigerinus*) tadpoles (N = 25 trials for each species). Data represents mean ± SE and analyzed by one-way ANOVA followed by Tukey HSD post-hoc test. Dissimilar letters above the bars indicate significant difference between the groups.

Discussion

In aquatic environments, most prey organisms including anuran tadpoles live under great predation pressure. This results in the evolution of defense means to escape from predation and promote survival (Schmidt and Amezquita 2001, Relyea 2007). The results of this study showed that species and refuge site act independently and do not interact hence they independently affect the larval survival following their encounter with the predator, *H. tigerinus.* Both in the absence and the presence of refugia, *D. melanostictus* tadpoles fell prey to *H. tigerinus* more easily than *U. taprobanicus* tadpoles. A main difference between the two prey species is the speed of swimming; the V_{max} of *D. melanostictus* tadpoles (13.58 cm/s) is lower than that of *U. taprobanicus* tadpoles (24.89 cm/s). Hence, *D. melanostictus* tadpoles are more susceptible to capture by predators than are *U. taprobanicus* tadpoles. Alternatively, it is also possible that better spatial avoidance by *U. taprobanicus* tadpoles or a preference of *H. tigerinus* to consume *U. taprobanicus* tadpoles over *D. melanostictus*. Our results conform to those of earlier studies (Van Buskirk and McCollum 2000, Dayton *et al.* 2005, Mogali *et al.* 2021). From the results of the present study it is clear that the V_{max} of predator, *H. tigerinus* tadpoles (60.21 cm/s) is much higher than both prey species hence it could capture both prey tadpole species easily. Irrespective of its high V_{max}, why do predator tadpoles preferably capture more *D. melanostictus* tadpoles than *U. taprobanicus* tadpoles? The answer might be predator put less effort to capture its prey (the one with low V_{max} i.e., *D. melanostictus*) and thus predator might conserve its energy for its growth and development. Alternatively, it could also be that capturing the slower prey is a good strategy to maximize the predator's energy intake rate (e.g., following the predations from optimal foraging theory; Werner and Hall 1974). It is generally believed that refugia reduce predation risk (Nystrom and Abjornsson 2000, Hossie and Murray 2010, 2011, Mogali *et al.* 2019, 2022). In the present study, we randomly observed the experimental tubs only during the day time, and we eye-witnessed that, basically both prey tadpole species used refuge sites when available as a consequence in the present study, in general, the susceptibility of both tadpole species was lower where refuge sites were available. Also, we have seen that *U. taprobanicus* tadpoles used more refuge sites or spent more time in refugia than that of *D. melanostictus* tadpoles. The position of the rearing tubs was randomized and changed daily to rule out position effects, if any.

In conclusion, the present study showed that *D. melanostictus* tadpoles are more susceptible to predators than those of *U. taprobanicus.* The present study on relative susceptibility of tadpoles of *U. taprobanicus* and *D. melanostictus* was conducted only at early larval stages of development (Gosner stages 26–27). The susceptibility of the two species may change over time. Further studies comparing the species throughout development are therefore needed. The finding of the present study clearly shows that at early stages of development, *U. taprobanicus* tadpoles have developed better predator avoidance behavior than that of *D. melanostictus* tadpoles.

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