

Are you experienced? Predator type and predator experience trade-offs in relation to tadpole mortality rates

F. Nomura¹, V. H. M. do Prado², F. R. da Silva², R. E. Borges³, N. Y. N. Dias⁴ & D. de C. Rossa-Feres²

¹ Departamento de Ecologia, Universidade Federal de Goiás, Goiânia, GO, Brazil

² Universidade Estadual Paulista, UNESP, São José do Rio Preto, SP, Brazil

³ Universidade de Rio Verde, FESURV, Fazenda Fontes do Saber, Rio Verde, GO, Brazil

⁴ Programa de Pós-Graduação em Zoologia, Departamento de Vertebrados, Universidade Federal do Rio de Janeiro, UFRJ, Museu Nacional, Quinta da Boa Vista, Rio de Janeiro, RJ, Brazil

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Correspondence

Fausto Nomura, Departamento de Ecologia, Universidade Federal de Goiás, UFG, Cx. Postal 131, St. Itatiaia, CEP 74001-970, Goiânia, GO, Brazil.
Email: fausto_nomura@yahoo.com.br

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Abstract

Cryptic behavior and unpalatability are common defensive strategies that occur in different taxonomic groups, but the effectiveness of these defensive strategies is context dependent, varying with predator type and co-occurring species. We tested this assumption by measuring the mortality rates of *Eupemphix nattereri* (cryptic behavior) and *Rhinella schneideri* (unpalatable) tadpoles in association with the predatory fish *Oreochromis niloticus* (vertebrate) and the dragonfly larvae of *Aeshna* sp. (invertebrate). We designed a second experiment to evaluate whether fish predators are capable of learning to avoid unpalatable prey once they have encountered it. Our results showed that fish preyed selectively on palatable tadpoles, avoiding unpalatable tadpoles and that the odonate larvae were more efficient in preying on the more active unpalatable tadpoles and less efficient in capturing those tadpoles that presented cryptic behaviors. Additionally, our data suggest that the antipredator traits of tadpoles can interact with each other, with cryptic tadpoles showing lesser mortality when co-occurring with unpalatable tadpoles and odonate predators. Unpalatable tadpoles also increase the mortality of cryptic tadpoles in the presence of experienced fish predators. These prey traits interact in modifying the prey preference of the predator, which constitutes a prey-induced trait-mediated interaction (TMI). This type of TMI is dependent on the system complexity (number of predator and prey species interactions) and could define food web properties, such as the role of predators and the number of competitor species in the system.

Introduction

We can visualize ecological communities as organized chains of interacting carnivores, herbivores and plants (Fretwell, 1987). In this food web context, prey have the ability to discriminate among predator-specific threats (Schmitz, Krivan & Ovadia, 2004), the predator–prey interaction being the basic direct interaction link between two species. The comprehension of this basic relationship is necessary for understanding other community properties (Werner & Peacor, 2003) and to know whether behavioral responses toward predators can generate predictable patterns of species distribution (Binckley & Resetarits, 2003; Steffan & Snyder, 2010).

Anuran tadpoles present a suitable model for studying predator–prey interactions because they represent a food source for a number of different vertebrates (birds, turtles, amphibians and fish) and invertebrates (beetle larvae, water bugs, dragonfly larvae and spiders) that show different foraging strategies (sit-and-wait or active foraging) and

several levels of sensitivity to unpalatability (Heyer & Muedeking, 1976; Morin, 1987; Wellborn, Skelly & Werner, 1996; Alford, 1999; Hero *et al.*, 2001). Generally, tadpoles present two types of defense mechanisms (*sensu* Brodie Jr, Formanowicz & Brodie, 1991): those that reduce the chance of encounters with predators (predator avoidance mechanisms), and those that reduce the predators' capture success (antipredator mechanisms). Predator avoidance mechanisms are generally behavioral (e.g. changes in the time of activity or in the foraging micro-habitat), whereas antipredator mechanisms can be behavioral, physiological or morphological (e.g. immobility or unpalatability) (Brodie Jr *et al.*, 1991). Several studies have shown the importance of predator–prey interactions in tadpole distribution patterns among different bodies of water (e.g. Hero, Gascon & Magnusson, 1998; Azevedo-Ramos & Magnusson, 1999; Azevedo-Ramos, Magnusson & Bayliss, 1999), and they have suggested that antipredator mechanisms are fundamental for explaining the coexistence of tadpoles with their predators (Hero *et al.*, 2001).

Several sources show that a tadpole's coloration is related to its antipredator mechanism. Unpalatable tadpoles present black coloration, which is generally associated to aposematism (Heyer, McDiarmid & Weigmann, 1975; Crossland & Alford, 1998; Crossland & Azevedo-Ramos, 1999; Hero *et al.*, 2001). Additionally, unpalatable black tadpoles do not show strong reductions in foraging activity upon perceiving predation risk (D'Heursel & Haddad, 1999; Jara & Perotti, 2009, 2010). In contrast, tadpoles with brown coloration usually exhibit cryptic behaviors, staying motionless in the presence of a predator and moving from one point to another at high speeds if the predator attacks (Heyer *et al.*, 1975; Azevedo-Ramos *et al.*, 1992; Nomura, Rossa-Feres & Prado, 2006). Unpalatability mechanisms are the main defensive trait that makes the coexistence of tadpoles and fish possible (Hero *et al.*, 2001) because fish are considered to be the main predators of tadpoles in permanent water bodies, such as pools and lakes (Heyer *et al.*, 1975). Nevertheless, the conspicuous coloration of unpalatable tadpoles increase their chances of encountering a predator (Azevedo-Ramos *et al.*, 1992; Chovanec, 1992; Hero *et al.*, 2001). Thus, because palatability does not restrict the consumption of tadpoles by many kinds of dragonfly larvae as it does for fish species (Crossland & Alford, 1998; Crossland & Azevedo-Ramos, 1999), dragonfly larvae are one of the most important predators of tadpoles among invertebrates (Gascon, 1992; Hero *et al.*, 2001; Gunzburger & Travis, 2004) and they can restrict the presence of unpalatable tadpoles in bodies of water (Hero *et al.*, 2001). However, tadpoles' cryptic behaviors are efficient to these invertebrate predators because the dragonfly larvae are sit-and-wait predators, and they are guided by a mixture of tactile and visual clues generated by the prey's movements (Pritchard, 1965; Azevedo-Ramos *et al.*, 1992). Owing to these differences, the efficiency of each strategy (unpalatability or crypsis) should vary according to the type of predator (vertebrate or invertebrate) (Hero *et al.*, 2001).

In this study, we tested whether the tadpoles of *Eupemphix nattereri* (crypsis) and *Rhinella schneideri* (unpalatability), which present different antipredator mechanisms, have different mortality rates depending on the predator type, the fish *Oreochromis niloticus* and the dragonfly larvae of *Aeshna* sp. Our hypothesis is that the efficiency of the antipredation strategy will be affected by the predator types: cryptic behavior will have higher success rates against the invertebrate predator, whereas unpalatability will have better success against the vertebrate predator. As suggested by Gunzburger & Travis (2005), once it has been established that a prey species is unpalatable to a predator, an experiment should be conducted to evaluate whether predators are capable of distinguishing palatable from unpalatable prey and are able to learn to avoid unpalatable prey once they have encountered it. Thus, we evaluated the ability of the fish predator to distinguish palatable from unpalatable prey but we also hypothesized that the experience of the predator and the antipredator mechanisms should interact and that the outcome of this interaction is dependent on the efficiency

of the mechanism used to avoid predation. Thus, we designed two simple experiments to answer the following questions: (1) are tadpole antipredator behaviors designed for encounters with a specific predator, thus representing differential survival strategies?; (2) is there any difference in tadpole mortality rates between experienced and inexperienced predators according to the type of antipredator mechanism exhibited by the tadpole?

Methods

Recently hatched tadpoles (*E. nattereri* and *R. schneideri*) and dragonfly larvae (*Aeshna* sp.) used in our experiments were collected in October 2006 from temporary ponds in Nova Itapirema (21°04'S; 49°31'W), São Paulo, Brazil. Fish (*O. niloticus*) were collected 5 days before starting the experiment from pisci-culture tanks at the Universidade Estadual Paulista (UNESP), São José do Rio Preto, São Paulo, Brazil. Although *O. niloticus* evolved on a different continent than the tadpoles used in our experiments, this species was introduced in Brazil in the 1970s for food production and is now found in natural systems (Gomiero & Braga, 2006; Langeani *et al.*, 2007). However, there is evidence in the literature that sensitivity to toxic substances among predators are interchangeable among continents because there is a phylogenetic constraint in the evolution of these toxic substances (metabolic pathways) as an antipredator strategy (Grant *et al.*, 2006; Maciel *et al.*, 2006). Additionally, this fish species is a suitable model for a tadpole predator because of its omnivorous feeding habits and association with benthic substrates (Froese & Pauly, 2010). No fish predator used in the experiments had previous experience with tadpoles of any anuran species. The tadpoles and fish were maintained in a laboratory and fed commercial fish food, whereas dragonfly larvae were fed Coenagrionidae larvae. To reduce manipulations of the experimental subjects prior to their use in the experiments, predators were standardized by size [odonate larvae size: mean \pm SD (range) = 48.42 \pm 3.38 mm (43.97–53.42 mm), n = 12] and tadpoles were less than one-third of the size of *Aeshna* sp. larvae [tadpoles size: mean \pm SD (range): 12.85 \pm 1.3 mm (10.28–15.0 mm); n = 480]. This was done to exclude the effect of tadpole size on their mortality rates. The same size range of tadpoles used with *Aeshna* sp. predators (10.0–15.0 mm) was used for fish predators (fish size range = 10.5–12 cm). All experiments were conducted using aged tap water and all tadpoles were of stage 25–26 (*sensu* Gosner 1960).

Predation experiment

These experiments were conducted in polyethylene containers of 29.5 \times 17.0 \times 9.0 cm, containing 1 L of water for odonate larvae (n = 12), or containers of 37.0 \times 30.0 \times 13.5 cm containing 4 L of water for fish (n = 12). For *Aeshna* sp., we provided perches made of plastic pipes distributed homogeneously along the polyethylene container to simulate the substratum used by the dragonfly larvae when

foraging. Predators were held individually for 24 h before the experiment to standardize their hunger levels. After this period, we added 10 *E. nattereri* and 10 *R. schneideri* tadpoles to the containers with *Aeshna* sp. and 40 tadpoles of both species to the containers with *O. niloticus* predators to maintain the same prey density in each treatment (20 tadpoles L⁻¹). The experiments were carried out for 30 min, after which the predators and surviving tadpoles were anesthetized and killed. All tadpoles were deposited in the DZSJRP-Amphibia collection, *O. niloticus* in the DZSJRP-Pisces collection and *Aeshna* sp. larvae in the DZSJRP-Insecta collection of UNESP.

Experience experiment

These experiments were conducted in polyethylene containers of 37.0 × 30.0 × 13.5 cm containing 4 L of water ($n = 12$). We tested the experience of the fish predators in response to unpalatable tadpoles. We compared the predation rates on *E. nattereri* and *R. schneideri* tadpoles by fish without any prior contact with tadpoles ($n = 8$) and by fish with previous contact with unpalatable tadpoles ($n = 8$). Fishes were fed with commercial fish food, but to provide experience with unpalatability and cryptic behavior, we offered as food 40 tadpoles of *E. nattereri* and 40 of *R. schneideri* for 6 h. After this time, all tadpoles remaining alive were removed, and the water in the aquaria changed. Fishes fed only with commercial fish food were considered inexperienced and those fed with tadpoles were considered experienced. To set up the experiments, we used the methods described above (predators and prey used only once, 40 tadpoles of each species available to the predator, and 24 h of standardization used for the hunger level) with 1-h experiment duration. At the end of the experiments, all specimens were anesthetized and killed and tadpoles were deposited in the DZSJRP-Amphibia collection and *O. niloticus* in the DZSJRP-Pisces collection of the UNESP.

Statistical analysis

We compared the mortality rate of tadpoles in the experiments using fixed-effect analyses of variance (ANOVA). For the predation experiment we used the predator type (two levels: dragonfly larvae and fish) and antipredator mechanisms (two levels: cryptic behavior and unpalatability) as fixed effects to test the null hypothesis that the mortality rates (response variable) of tadpoles would be the same. For the experience experiment we used the experience of the fish with tadpole antipredator mechanisms (two levels: with or without experience) and tadpole palatability (two levels: palatable and unpalatable) as fixed effects to test whether the mortality rates (response variable) of the tadpoles were the same. The data were arcsine transformed according to Freeman and Tukey (Zar, 1999) for variance homogenizations. Although this transformation was partially successful (Bartlett test for predation experiment: $K_{\text{grouped by predators}}^2 = 22.0672$, d.f. = 1, $P < 0.001$; $K_{\text{grouped by tadpoles}}^2 = 11.8926$, d.f. = 1, $P < 0.001$; Bartlett test for experience experiment:

$K_{\text{grouped by predator experience}}^2 = 0.8551$, d.f. = 1, $P = 0.3551$; $K_{\text{grouped by tadpoles}}^2 = 19.4145$, d.f. = 1, $P < 0.001$), we assumed that ANOVA is robust against violations of the assumption of variance homogeneity (Lindman, 1974). To evaluate our decision, we also performed a non-parametric two-way ANOVA to compare the medians of our dependent variable between groups, which produced similar results when compared to the parametric ANOVA. We presented the results of the parametric ANOVA, because the associated P -values, although statistically significant, were higher than those P -values generated by the non-parametric approach, adding higher confidence to the effects that we detected. Statistical analyses were performed with the STATISTICA 7.0 (StatSoft, 2004) software.

Results

Predation rate experiment

The predation rate on the two tadpole species differed between the treatments due to the predator type and to the tadpoles' antipredator mechanism (Table 1, Fig. 1). The rate of mortality of *E. nattereri* was higher than that of *R. schneideri* when the fish was the predator ($Enat_{\text{fish}} = 97.92\% \pm 7.22$; $Rsch_{\text{fish}} = 3.12\% \pm 2.64$), whereas *R. schneideri* was consumed at higher rates in the dragonfly treatment ($Enat_{\text{dragonfly}} = 78.33\% \pm 21.67$; $Rsch_{\text{dragonfly}} = 92.5\% \pm 9.65$). Overall, these results indicate that the rate of tadpole predation was influenced by the interaction of the predator type and the tadpole antipredator mechanisms (Table 1, Fig. 1).

Experience experiment

The mortality of *E. nattereri* tadpoles was higher than the mortality of *R. schneideri* tadpoles irrespective of fish experience ($Enat_{\text{mortality rate}} = 75.47\% \pm 22.70$, $Rsch_{\text{mortality rate}} = 1.72\% \pm 2.54$; Table 2, Fig. 2). Although we were unable to detect any significant difference in tadpole mortality solely based on fish experience ($Enat_{\text{inexperienced}} = 67.81\% \pm 26.54$, $Enat_{\text{experienced}} = 83.12\% \pm 16.30$, $Rsch_{\text{inexperienced}} = 3.44\% \pm 2.65$, $Rsch_{\text{experienced}} = 0.00\% \pm 0.00$; Table 2, Fig. 2), the interaction between the tadpole's antipredator mechanism and the fish's experience differed between the treatments (Table 2, Fig. 2).

Table 1 ANOVA factorial analysis with predator type (fish or odonata larvae), tadpole type (crypsis or unpalatability) and their interaction effects in the mortality rates of tadpoles

Source	SS	d.f.	MS	F-ratio	P
Predator type	1.48	1	1.48	60.27	<0.001
Tadpole type	3.82	1	3.82	155.43	<0.001
Predator × Tadpoles	6.54	1	6.54	266.40	<0.001
Error	1.08	44	0.03		

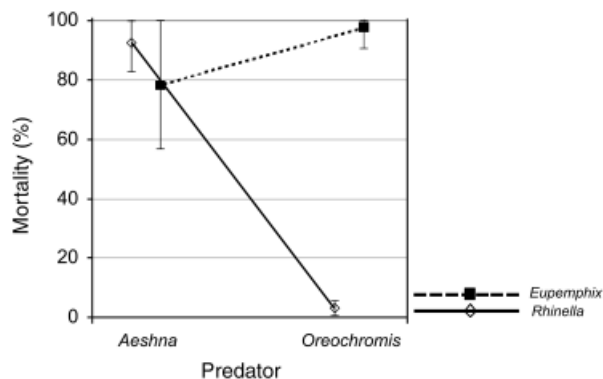


Figure 1 Per cent mortality \pm 1 SD of cryptic tadpoles (*Eupemphix nattereri*) and unpalatable tadpoles (*Rhinella schneideri*) in response to two predator types: fish (*Oreochromis niloticus*) and dragonfly larvae (*Aeshna* sp.).

Table 2 ANOVA factorial analysis with predator experience (experienced or non-experienced), tadpole type (cryptis or unpalatability) and their interaction effects in the mortality rates of tadpoles

Source	SS	d.f.	MS	F-ratio	P
Predator experience	0.010	1	0.010	0.259	0.615
Tadpole type	7.748	1	7.748	165.632	<0.001
Predator experience × Tadpoles	0.197	1	0.197	4.366	0.046
Error	1.264	28	0.050		

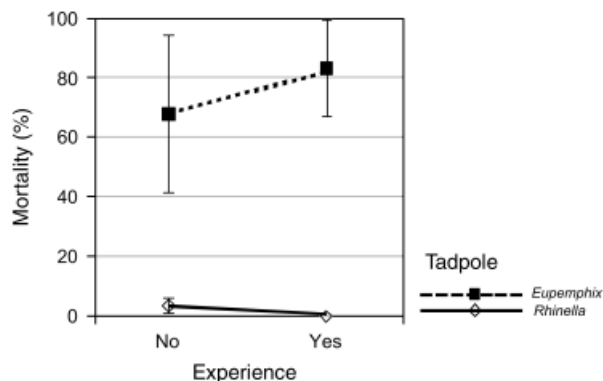


Figure 2 Per cent mortality \pm 1 SD of palatable tadpoles (*Eupemphix nattereri*) and unpalatable tadpoles (*Rhinella schneideri*) in response to inexperienced and experienced fish (*Oreochromis niloticus*).

Discussion

Behavioral trade-offs

In our experiments, fish preyed selectively on *E. nattereri*, avoiding the unpalatable *R. schneideri* tadpoles. Odonate larvae were more efficient in preying on the more active *R. schneideri* tadpoles, consuming fewer *E. nattereri*

tadpoles, which presented cryptic behavior. Therefore, the efficiency of the antipredator mechanism, measured by the mortality rate, was affected by the type of predator, being the unpalatability significantly more efficient in deterring predation by fish than by odonate predators, whereas cryptic behavior was more efficient against the odonate predator.

Differences in predatory behavior, such as prey detection thresholds, foraging mode and manipulation time, affect the efficiency of tadpoles' defense mechanisms and allow the establishment of behavioral trade-offs between predators and prey (Peckarsky, 1984; Wellborn *et al.*, 1996; Skelly, 1997). For example, both fish and dragonfly larva are visually oriented predators, but fish can detect prey from a greater distance and are more efficient to detect immobile prey than can dragonfly larvae (Wellborn *et al.*, 1996) which makes cryptic behavior more efficient against dragonfly larvae than against fish. In contrast, like some other odonate species (Ballengée & Sessions, 2009; F. Nomura, unpubl. data), the *Aeshna* sp. larvae that we used in our experiments were able to prey on unpalatable tadpoles by selectively feeding on the palatable parts as opposed to the unpalatable ones. This behavior allowed the odonate larvae to prey on tadpoles that were unpalatable and selectively avoided by fish, which makes unpalatability more efficient against the fish than against the dragonfly larvae. Thus, the predator traits and the tadpole antipredator mechanisms interact to determine the distribution and assemblage composition of anuran larvae (Hero *et al.*, 2001; Jara & Perotti, 2010) through a behavioral trade-off effect.

Trait-mediated interactions (TMI)

Our results suggest that the antipredator traits of tadpoles could affect the predation rates of co-occurring tadpole species, since these antipredator traits could modify the fish and the odonate larvae prey preferences. In our experiments, cryptic tadpoles have higher survivorship when co-existing with unpalatable tadpoles in the presence of *Aeshna* sp. predators and have lower survivorship when co-existing with unpalatable tadpoles in the presence of fish predators.

Many odonate predators are not affected by the skin toxins that make tadpoles unpalatable to fish (Crossland & Alford, 1998; Hero *et al.*, 2001; Smith *et al.*, 2008; Ballengée & Sessions, 2009). For these predators, our experiment demonstrated that the cryptic behavior was more efficient at avoiding predation. In temporary ponds, where fish are generally absent and the predation pressure of odonate predators can be substantial (Van Buskirk, 1988; Scheffer *et al.*, 2006; Jara & Perotti, 2010), the tadpole predation risk could be measured by the activity of the tadpole in the presence of the predator (Hero *et al.*, 2001). Thus, cryptic tadpoles could reduce their mortality by reducing their foraging activity (Hero *et al.*, 2001). However, as unpalatable tadpoles exhibit a slow but constant swimming activity pattern and show only a small reduction in their activity in the presence of predators (D'Heursel & Haddad, 1999; Hero *et al.*, 2001; Jara & Perotti, 2009, 2010; F. Nomura, unpubl.

data), the cryptic behavior also affects the predation risk of unpalatable tadpoles, making unpalatable tadpoles more easily detected by odonate predators.

Conversely, unpalatable tadpoles could modify the predator's prey preference, when the predator has some learning ability and is affected by its skin toxins. In our experience experiment, inexperienced fishes captured and rejected the *R. schneideri* tadpoles, sometimes chewing them before rejecting the tadpole (F. Nomura, pers. obs.). Although this behavior accounted for the majority of unpalatable tadpole mortality, experienced fish were never observed displaying this 'tasting' behavior (F. Nomura, pers. obs.). Despite the fact that the fish predators used are generalists, the prey preference of the fish was modified by unpalatability and improved by learning, because experienced fish learned to avoid unpalatable tadpoles, but they also learned to select and prey more efficiently on palatable tadpoles. Consequently, our results show that the experienced fish had a greater predation rate on *E. nattereri* compared with the inexperienced fish. As demonstrated by the previous experiment, cryptic behavior was not only ineffective against the fish, but it also became even less effective with fish experience.

These behavioral interactions are the main process that originate TMIs, which is the ability of an organism to modulate its behavior, improving a behavioral trait (e.g. evade a predator) with an associated reduction in another (e.g. reduction in foraging activity), in response to a trait component of another species (Bolnick & Preisser, 2005). TMIs are recognized as ubiquitous ecological phenomena, influencing not only how species interact but also how communities function (Schmitz *et al.*, 2004; Preisser *et al.*, 2005; Steffan & Sneider, 2010), originating top-down or bottom-up trophic cascades, and also mediating competitive interactions (for a review of TMI see Werner & Peacor, 2003; Schmitz *et al.*, 2004; Bolnick & Preisser, 2005). Our experiments demonstrate that the predation rate of tadpoles is strongly affected by TMI effects, since the tadpole behavior influences the predator's prey preference and learning. In this context, we observed the following: (1) TMI effects are highly context dependent because the subject affected is determined by the type of predator, by the antipredator mechanisms and by the competitors in the system (Werner & Peacor, 2003; Schmitz *et al.*, 2004); (2) there are also prey-induced TMI effects in predator-prey systems because the predator's prey preference is dependent on the prey's antipredator mechanism.

Context-dependent TMI effects are well known and have been demonstrated in various studies (Werner & Peacor, 2003; Schmitz *et al.*, 2004; Bolnick & Preisser, 2005); however, prey-induced TMIs are less well known. Prey-induced TMIs differ from bottom-up effects because the TMI is not triggered by feeding/risk trade-offs of the prey, that is, a predator trait modifying a prey behavior (predator-induced TMI; Werner & Peacor, 2003). Instead, the prey-induced TMI is triggered by prey preference/palatability or prey preference/prey encounter rate trade-offs of the predator, that is, a prey trait modifies a predator behavior (prey-

induced TMI). Because of this prey-induced TMI effect, the shift in the prey preferences of the predators results in selective predation and reduction/exclusion of the system of a potential competitor species. Despite the fact that the invertebrate or the fish predators used in our experiments can consume many types of prey species, they assume the role of specialist predators; the odonate larvae preying selectively on more active and, in general, unpalatable tadpoles and the fish preying on palatable and, in general, cryptic tadpoles.

Moreover, prey-induced TMI differs from the common three-species shared-predator web TMI response (Werner & Peacor, 2003) because the causal path of the prey-induced TMI is from one type of prey (unpalatable or cryptic) to the behavior (prey preference) of the predator, which then affects the predation risk of the other prey. Thus, the prey-induced TMI can, in addition to offering protection against predators, reduce the competition with other tadpole species that are vulnerable to the predator in the system.

Conclusion

We demonstrate that prey traits can also interact with predator prey-preference, which constitute a prey-induced TMI. This type of TMI is dependent on the complexity of the system (number of predator and prey species interactions) and could define food web properties, such as the predator role, and mediate competitive interactions.

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