



Space use and phenotypic plasticity in tadpoles under predation risk

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Abstract Food acquisition by most organisms is a complex ecological process that involves benefits and risks, affecting organism development and interspecific interactions. The evaluation of habitat selection, food consumption, and predator avoidance is pivotal for understanding the ecological process affecting life history traits and the role of species on communities and ecosystems. In a microcosm experiment, we evaluated if *Rhinella diptycha* tadpoles actively choose to forage in habitats with high resource (food) availability and if they avoid such habitats when predators are positively correlated with resource distribution. We also evaluated if behavioral changes

under predation risk were associated with specific morphological phenotypes. We observed that tadpoles chose, although not intensely, habitats with high resource availability when predator cues were absent, but they avoided the same habitats when predation cues were present. We also observed an increase in swimming activity and morphological changes in tadpoles exposed to predation risk, especially related to body and tail morphology, which translates into rapid development. Our results suggest that tadpoles assess habitat quality through resource availability and predation risk. Moreover, our results suggest that tadpoles seem to exhibit functionally independent co-specialization of defensive strategies, due to the expression of specific behavioral and morphological phenotypes.

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Introduction

The ability of organisms to move across ecosystems or habitats can affect ecological processes from the individual to the community level, such as population dynamics (Krivan, 2003), interspecific interactions (Schmidt et al., 2000), and persistence in disturbed environments (Pease et al., 1989; Hanski & Ovaskainen, 2000; Prevedello et al., 2010). To enhance fitness,

individuals may change their phenotype to better match local environmental conditions through physiological (Seebacher et al., 2015) and behavioral plastic responses (Wong & Candolin, 2015). However, individuals may also choose a suitable environment to fit their phenotype (e.g., Ravigné et al., 2009). In this “matching habitat choices” phenotypic plasticity can operate simultaneously with habitat choice to increase individual’s fitness (Edelaar et al., 2008).

The study of prey foraging behavior was paramount to the understanding of habitat selection (Kotler & Blaustein, 1995) and the trade-off between food acquisition and survival (Abrahams & Dill, 1989). Some studies based on the Ideal Free Distribution model for three trophic levels (predator that feeds on prey, which feeds on a fixed resource) (Kacelnik et al., 1992) verified the influence of predation risk in habitat use by prey (e.g., Caldwell, 1986; Ferguson et al., 1988; Turkia et al., 2018). They showed that prey should prefer sites with low-predator abundance, while predators commonly establish themselves in prey-rich environments (Lima & Dill, 1990; Lima, 1998), reaching an evolutionary stable strategy (ESS) where neither predator nor prey can increase their fitness by shifting their habitats (e.g., Van Baalen & Sabelis, 1993; Alonzo, 2002). Therefore, when assessing habitat patches, prey are trying to balance their foraging needs and the predation risk (Luttbeg & Sih, 2004; Guariento et al., 2014). However, it was previously shown that prey tend to distribute evenly among patches, regardless of the distribution of resources, when predators are free to move (Hammond et al., 2007). Such dynamic is commonly observed in aquatic habitats, where constant and persistent chemical cues released by predators or conspecifics can induce prey to develop specific behavioral strategies that would maximize their fitness (Perotti et al., 2006; Hammill & Beckerman, 2010).

Predation risk may also influence prey morphological traits (Kerfoot, 1987; Appleton & Palmer, 1988; McCollum & Leimberger, 1997). For instance, an environment with predators induces the development of protective structures (e.g., spines in water fleas; Repka & Pihlajamaa, 1996; Dewitt et al., 2000) and changes in body features in prey (e.g., shortening tentacles in sea anemones; Howe & Sheikh, 1975). However, many prey express more than one predator-inducible defense when facing predation risk (Chivers & Smith, 1998), and such defenses are likely to be

correlated. In other words, behavioral and morphological responses to predation risk tend to be co-expressed, suggesting that prey behavioral responses do not limit their ability to respond morphologically. Such a positive correlation between behavioral and morphological responses indicates that trait co-specialization may be a predominant pattern in nature, maximizing survival through co-activation of multiple independent phenotypes (Hossie et al., 2017).

Using an experimental microcosm, we assessed if tadpoles of *Rhinella diptycha* (Cope, 1862) (Anura: Bufonidae) actively choose to forage in habitats with higher resource availability and if they avoid such habitats when dragonfly nymphs’ predators are present. These tadpoles inhabit benthic temporary ponds and rapidly reach the metamorphosis before the pond dries up (McDiamird & Altig, 1999; Wells, 2010). These organisms also present some unpalatability (Wassersug, 1971; Nomura et al., 2011). However, this unpalatability does not prevent the consumption of these tadpoles by dragonfly larvae (Crossland & Azevedo-Ramos, 1999; Gunzburger & Travis, 2004). When threatened, they usually reduce their activity and adopt a gregarious behavior, as documented for other tadpoles of the genus *Rhinella* (Skelly & Werner, 1990; Perotti et al., 2006; Stav et al., 2007; Jara & Perotti, 2010). Such behavioral responses and short metamorphosis cycle make *R. diptycha* tadpoles good experimental models to evaluate behavioral and morphological plasticity. Considering the trade-off between predation risk and energy acquisition (Abrahams & Dill, 1989; Lima, 1998; Hammond et al., 2007), we aimed to test (i) whether tadpoles avoid patches with high resource availability and high predation risk and (ii) whether shifts in behavioral patterns are associated with morphological plastic responses to predation risk. We hypothesized that tadpoles choose low-resource patches over high resource patches when predation risk is present at high resource patches and the perceived risk of predation leads to behavioral responses coupled with morphological changes in tadpoles.

Materials and methods

We collected individuals of *Rhinella diptycha* tadpoles and dragonfly nymphs of the genus *Erythrodiplax* (Odonata: Libellulidae), a natural

predator of tadpoles (Hero et al., 2001). Tadpoles and dragonfly nymphs were sampled with sieves in permanent puddles in the Lago do Amor, a lake inside the campus of the Federal University of Mato Grosso do Sul, Brazil (20°30'16.64"S, 54°36'55.60"W). Both organisms are abundant in ponds in the Mato Grosso do Sul State (Rodrigues & Roque, 2017; Souza et al., 2017). We conducted the experiment in ten indoor arenas (plastic boxes of 56 × 42 × 13 cm) filled with seven liters of aged tap water. Our arenas were similar (e.g., Relyea, 2001; Luttbeg et al., 2008) or even bigger (e.g., Nomura et al., 2011) in size and water volume to those used in previous studies on morphologic and behavioral plasticity. We placed pellets of food resource (scrunched rabbit chow mixed with unflavored gelatin) at each side of the arena. One patch had high food availability (three portions of chow, totaling 0.5416 g) and another patch had low food availability (half of one portion of chow, with 0.0902 g) (see Luttbeg et al., 2008). We considered as a patch each half of the experimental arenas. In each arena, we introduced five tadpoles in stages 24 to 26 (Gosner, 1960) with similar length (mean ± SE = 26.88 ± 1.75 mm) and showing feeding behavior. For all 10 arenas, the resource distribution was the same, with different food patches at each side of the arenas. However, for five of the ten arenas, at one side we placed one caged predator in a cage made of a transparent polyethylene terephthalate (PET) bottle, creating a two-level risk treatment, with and without predators, with five replicates each. The other five arenas were the replicates of our control treatment, with no cages or predators. PET bottles were 9.5 cm in diameter and presented small holes that allowed water exchange. The cage with the predator was always attached next to the patch with high food availability. Such configuration was due to the fact that predators usually choose patches with high resource availability in spatial predator–prey arrays (Luttbeg et al., 2008). On the other side of the arena with the predator, we placed a predator-free cage, as a control for the cage effect. With such an arrangement, we create a trade-off between predation risk and energy uptake in the experimental arenas where predators were present, maintaining the distinct food distribution within each replicate (Fig. 1). Predator and prey were placed in the arenas to acclimation for 24 h before the beginning of the experiment and we fed predators with one *R. diptycha* tadpole three times, daily. The temperature of

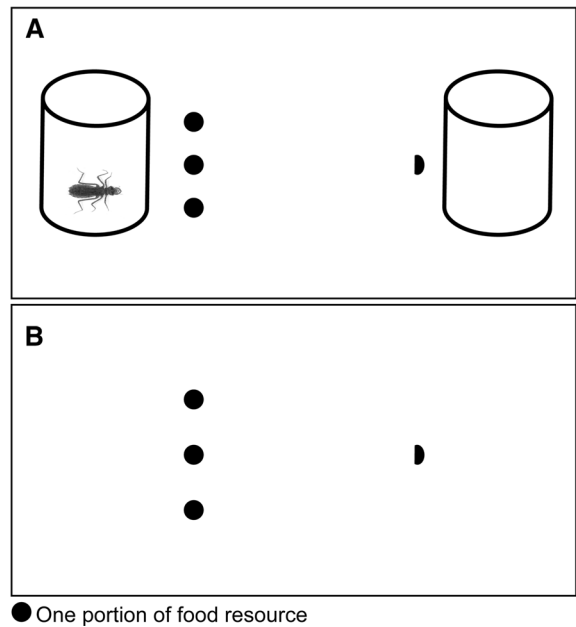


Fig. 1 Illustrative scheme of the experimental units. **A** Predation risk treatment ($N = 5$), with predator associated with the patch with abundant resources and **B** predator-free treatment ($N = 5$). The cage in the predation risk treatment had several small holes to permit the water flow inside the cage and spread the chemical cues released by the predator

water in the experimental units ranged from 26.3 to 27.5°C (room temperature).

For 5 days, we conducted 12-morning observations per day at intervals of 20 min between each observation. For each observation, we recorded prey's spatial distribution and behavior patterns (swimming activity). We quantified the spatial distribution by counting the number of individuals in each patch (patch occupancy proportion) and counting the active tadpoles. We did not consider as active those tadpoles that were just moving the tail but remained still. At the end of the experiment, we euthanized the tadpoles in a freezer at -20°C (cryoanesthesia) and measured seven external morphological variables (tail length—TL, tail depth—TD, body depth—BD, tail muscle depth—MD, body length—BL, tail width—TW, body width—BW; Fig. 2) to evaluate the plasticity of morphological responses of tadpoles under predator pressure. We measured the tadpoles from photographs taken by a computerized magnifying scope (Zeiss® Discovery V20) using the ZEN 2 (blue edition) Imaging Software. We made the photographs with the tadpoles submerged in 70% alcohol in a petri dish,

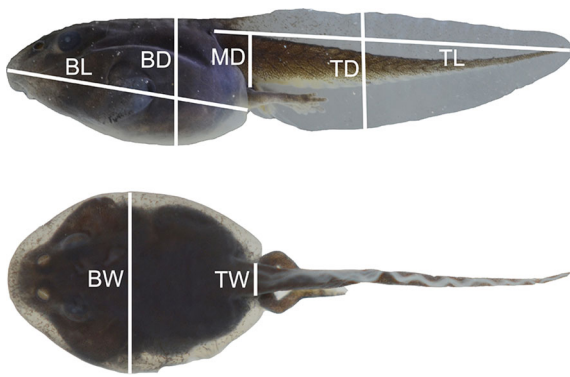


Fig. 2 Side view (above) and dorsal view (below) of a *Rhinella diptycha* tadpole illustrating the seven linear measures taken for morphological plasticity analysis (tail length—TL, tail depth—TD, body depth—BD, tail muscle depth—MD, body length—BL, tail width—TW, body width—BW). We used a tadpole at Gosner stage 37 for a better visualization of the measured morphological variables

keeping the scope lenses and tadpoles at a standard focal length. Because putting tadpoles in alcohol after freezing may distort its size and shape, each tadpole was photographed in an acclimatized room immediately after being removed from the freezer.

Data analysis

To verify if the amount of food (resource) and predators affect the distribution of tadpoles in the experimental arenas, we compared the occupancy in the same patch type (i.e., high resource patch) between treatments. Since we have only two patches in each experimental arena, the proportion of tadpoles on each side of the arenas is directly dependent on each other. Therefore, as a response variable, we focused exclusively on the proportion of the occupancy on the high resource patch, avoiding including the dependency of patch types within treatment levels in our analysis. To analyze the effects of predation risk on prey habitat choice, we used a binomial generalized linear mixed model (function `glmmPQL` from package `MASS` in R 3.5.1), where tadpoles' occupancy proportion in the high resource patch was used as the response variable. The predator presence was used as a fixed predictor variable and the different days of observation were used as a random factor. Although in this work we do not explore the temporal effect of predation risk, mostly due to the short overall extension of our experiment, we used the factor “time” to remove the

error associated with different days of observation, to adjust the degrees of freedom of the analysis, and to avoid pseudoreplication due to multiple observations for the same experimental unit (Davies & Gray, 2015). We also conducted a one-sample *t* test only to test the overall tendency of tadpoles to occupy the high resources patch in the absence of predator. To evaluate the consistency of the risk effect along the experimental period, without inflating the model degrees of freedom, the variable “risk” was treated as nested inside the random variable time (Davies & Gray, 2015). After applying our statistical model to the data, we conducted a visual inspection of the distribution of residuals and variance among treatments to confirm that the model was appropriate. We also compared our model results with the results of a model with a “quasi-binomial” distribution, to evaluate for a possible data overdispersion. As we found a similar variance among treatments and we did not detect overdispersion, we assumed that the original model was suitable. We used the same statistical approach to analyze the effects of predation risk on swimming activity. However, in this case, the proportion of active animals in the arenas was treated as a response variable.

We conducted a principal component analysis (PCA) to evaluate tadpoles' morphological differences among treatments (Bookstein, 1997; McCoy et al., 2006). To test for significant differences on overall tadpoles' morphology among risk treatments, we used the two axes with higher variance from the PCA analysis in a MANOVA, where the presence and the absence of predators were treated as a predictor variable. The average value of all traits for both treatments is available on the Online Resource 1.

In order to verify the consistency of experimental manipulations throughout the experiment, we measured the total resource mass in each patch at the end of the experiment. We used the difference between initial and final mass, relative to the total mass, as a measure of resource decay and used an ANOVA to evaluate if the resource decay varied between patches among treatments with and without predation risk. All statistical analyses were performed in R 3.5.1 (R Development Core Team, 2016).

Results

Activity and habitat selection

Tadpoles slightly tended to prefer the high resource patch with no predation risk throughout the experiment, which was more evident at the end of the experiment (Online Resource 2). Without predation risk, on average, 57% of tadpoles occupied patches with high resource (Fig. 3A), which was significantly

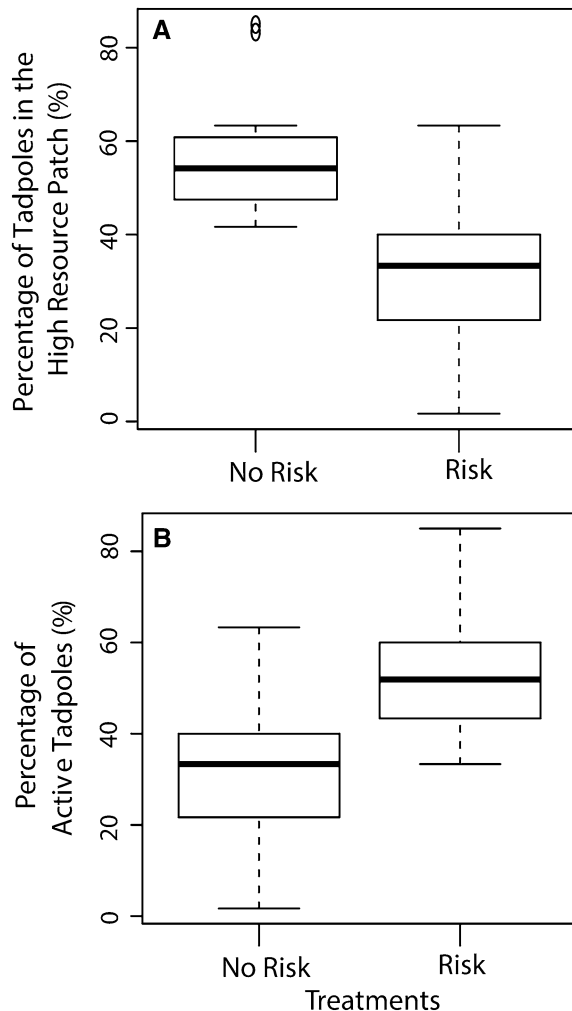


Fig. 3 **A** Box plot showing the mean and standard error of prey habitat use, where we observe that the use of high resource patch in risk treatment was higher than in control treatment. **B** Box plot showing the mean and standard error of tadpoles' activity between the treatments. Tadpoles exposed to caged predator presented more mean activity proportion (swimming or feeding) than those tadpoles in the risk-free boxes. The open circles represent the outliers

different from the 50% threshold ($t = 2.66$, $df = 5$, $P = 0.007$). With predation risk, on average, only 37% of tadpoles occupied patches with high resource (Fig. 3A). We observed that patch choice by prey was significantly affected by the presence of the predator (Fig. 3A; $t = -4.90$, $df = 5$, $P = 0.004$). We also found that predation risk significantly affected tadpoles' activity (Fig. 3B; $t = 3.41$, $df = 5$, $P = 0.02$), with an average of 52% and 34% of the tadpoles presenting high swimming activity in the risk treatment and in the risk-free treatment, respectively.

Food consumption

We found that the two main effects of our experiment did not influence the food intake by tadpoles (Predation risk: $F = 0.20$, $df = 1$, $P = 0.66$ and food availability: $F = 2.20$, $df = 1$, $P = 0.15$). The average of remaining food in the risk treatment was 0.059 g (89.11% of food consumption) and 0.018 g in the risk-free treatment (86.04% of food consumption). We also did not find any significant interaction among the main effects ($F = 0.94$, $df = 1$, $P = 0.34$), indicating that tadpoles fed proportionally on both sides of the arena.

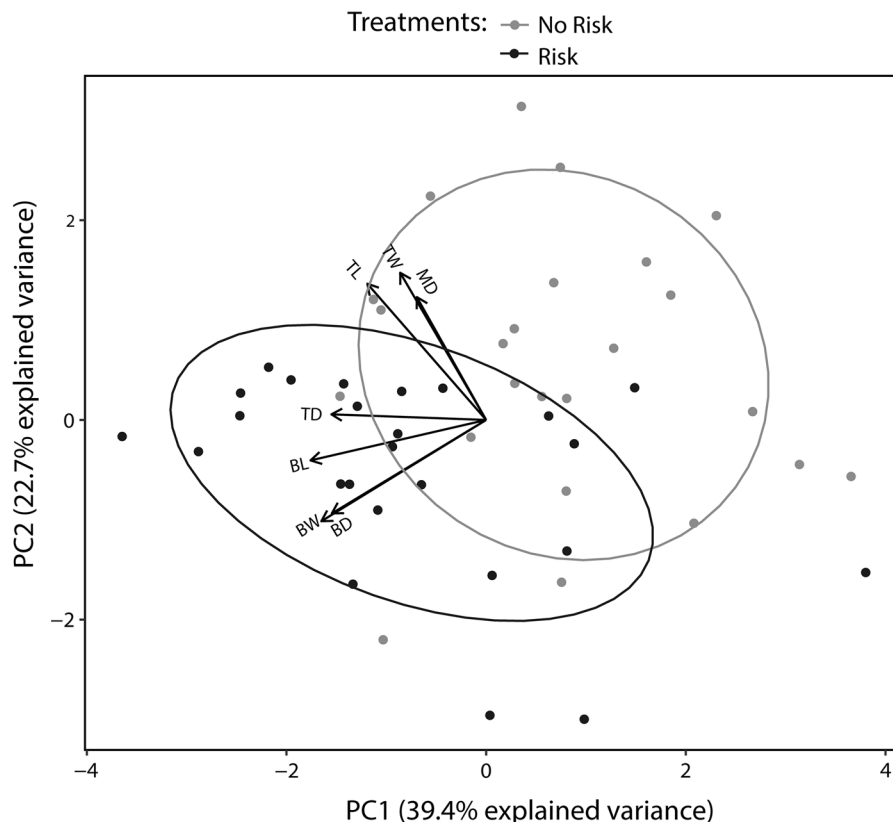
Morphological attributes

The two first axes of PCA comprised of 62.1% of the variation in tadpoles' morphological characters. PCA scores of distinct treatments on the ordination space are not completely overlapped; this indicates that tadpoles from different treatments present distinct morphologies. We observed that the scores for risk treatments are correlated with vector plots for BD, TD, BL, and BW. This show that in the treatments with predation risk, tadpoles have larger BD, TD, BL, and BW compared to treatment with no risk. The MANOVA revealed that tadpoles exposed to predation risk have, indeed, significantly distinct PCA scores compared to risk-free treatments (Fig. 4; $F = 15.48$, $df = 2$, $P = 7.20 \times 10^{-6}$). A table with all morphometric measures is available on the Online Resource 3.

Discussion

Tadpoles tended to choose patches with low food availability when exposed to predation risk, while

Fig. 4 Summary PCA biplot of the morphological data (tail length—TL, tail depth—TD, body depth—BD, tail muscle depth—MD, body length—BL, tail width—TW, body width—BW) among predation risk treatments



those in the risk-free treatment tended to use patches with high resource availability. These findings agree with our first hypothesis and previous studies showing that consumers prefer foraging in high-quality patches in the absence of predation risk (Brown et al., 2001; Shrader et al., 2012). We also corroborated our second hypothesis that both behavioral and morphological traits displayed under predation risk are consistent with an adaptive response to faster ontogenetic development (McCollum & Leimberger, 1997; Relyea, 2001; Van Buskirk & Arioli, 2002; Eklöv & Svanbak, 2006). However, instead of a typical activity reduction, tadpoles under predation risk spent more time being active.

The selection of patches without predation risk rather than patches with predation risk represents an adaptive mechanism that ultimately translates into higher fitness (Luttbegg & Sih, 2004), even in the short term (Winandy et al., 2017). Our study was designed to represent a partial test of Ideal Free Distribution theory (Godin & Keenleyside, 1984; Krivan, 1997), which predicts that prey should prefer patches richer in

resources, but when predator presence is correlated to resources, prey will be uniformly distributed among the available patches (Hammond et al., 2007). We observed that *R. diptycha* tadpoles assess a habitat not only based on the quality or amount of resources, but also on predation risk (Werner et al., 1983; McIvor & Odum, 1988; Heithaus & Dill, 2002). However, as shown in previous studies, prey might choose high-risk patches if they are energetically profitable toward the costs imposed by predation risk (Gotceitas, 1990; Scrimgeour et al., 1994). For example, Peterson & Skilleter (1994) observed that the facultative suspension/deposit feeder mussels *Macoma balthica* (Linnaeus, 1758) choose to feed in profitable but dangerous substrates if their siphons, an exposed feeding organ, has not been cropped by a predator fish. If their siphons are cropped, they must leave their shells to forage in the water column, where resources are lower, but also predation risk. Despite the fact that *R. diptycha* tadpoles avoided high-quality patch due to predation risk, the amount of resources and the susceptibility to predation may vary depending on

predator identity (Bernot & Turner, 2001), which affects prey decisions. This might explain why tadpoles were not uniformly distributed but instead, shifted their distribution to the low-resource patch under predation risk. We would like to highlight that although we found an evidence that tadpoles choose to occupy the richer resources habitat (57% of tadpoles on average), when no predator was present, such effect was relatively small. Perhaps, our experimental design resulted in a small difference between the resource quantities among patches, which translated into a weak effect on tadpoles' preference for the more resourceful habitat throughout the experiment. Further studies should test the effects of the difference in the amount of resource availability among patches on prey habitat preference, and/or to manipulate the resource quality, comparing the effects of more nutritional against poor nutritional resources on prey habitat use under predation risk (Hammond et al., 2007; Guariento et al., 2018).

Tadpoles exposed to predation risk increased their overall activity, the opposite result of previous studies that showed a reduction in tadpoles' swimming activity and food consumption in response to predation risk (Jara & Perotti, 2010; Takahara et al., 2013; Anderson & Lawler, 2016). Despite the observed effects of predation risk on tadpole's distribution, we found that the proportional rates of food consumption were similar for both risk and risk-free treatments. We argue that a potential increase in tadpoles' displacement into the risky patch may be due to an attempt to increase resources intake (Lima & Dill, 1990), and thus rush development to leave the hostile habitat (Relyea & Hoverman, 2003; Costello & Michel, 2013). An unappreciated perspective is the fact that temporal variation in risk may be a fundamental driver behind predation risk-dependent behavior. As a consequence of this variation in risk, animals are generally faced with the problem of how to best allocate feeding and antipredator efforts across different risk states (Lima & Bednekoff, 1999). In the present experiment, we were not able to fine-track individual patterns of food consumption by tadpoles mainly because *R. diptycha* tadpoles can forage continually during the diel cycle (McDiarmid & Altig, 1999). Despite the fact that we did not intensively record the foraging activity of tadpoles, the absence of difference in the proportional food intake among treatments may be due to the fact that the costs of reduced feeding at

certain periods may be compensated by increased foraging at other periods. For example, predator inactivity may reduce the concentration of chemical cues in the water (Van Buskirk et al., 2014), therefore, prey may change their feeding patterns (e.g., through differential activity or space distribution) when predator is inactive, and employ antipredator efforts at contrasting circumstances.

Based on the observed results, we argue that the observed behavioral and morphological responses in *R. diptycha* tadpoles represent a co-adaptation of successful anti-predatory plastic defenses (Hossie et al., 2017), maximizing predator avoidance through habitat selection and development acceleration. The investment in deeper tail fins (TD) increases the chance of predators attacking tadpoles in a soft part of the tail rather than the head and body regions, allowing them to escape more easily (Van Buskirk et al., 2003). Furthermore, the investment in specific body changes (BL, BD, and BW) is consistent with faster metamorphosis, which facilitates tadpoles to leave an unfavorable environment more quickly (Relyea, 2001). Temporary ponds commonly harbor different aquatic predators with a wide variety of hunting strategies, and prey with several mechanisms of defenses (Peckarsky, 1982). To date, most of the empirical work on phenotypic plasticity has focused on single-trait responses (Pigliucci, 2005) and is becoming increasingly important to understand how the plastic responses of organisms vary in response to multiple environmental factors (DeWitt & Langerhans, 2003; Pigliucci, 2003). The simultaneous expression of behavioral and morphological traits observed in our experiment should, therefore, indicate that trait co-specialization is a predominant pattern of defense in these larval amphibians, as observed for other different species (Hossie et al., 2017). This result might represent a likely adaptive response of preys to deal with multiple predation threats in their habitats.

At last, the existence of a relationship between habitat quality and animal behavior may improve our understanding on habitat selection, which, therefore, affects the spatial distribution of an organism (Boyce et al., 2016). Studying habitat choice is particularly relevant in species with complex life cycles, requiring the evaluation of both reproduction strategies and movement, within and across habitats, to better describe the suite of behavioral strategies employed in habitat selection (Winandy et al., 2017). Overall, we

claim that behavioral and morphological phenotypic responses of tadpoles may be relevant to species with short life cycles in the aquatic environment, such as *R. diptycha*. However, species with long life cycles in aquatic environments, such as species of the genus *Lithobates*, may invest in traits that improve their ability to deal with predators, such as increased tail muscle width, to increase natatorial efficiency (Guariento et al., 2015). Despite this proposed scenario, such a premise remains to be tested in future studies that can explicitly compare the response of different species categorized in short- or long-term aquatic life cycles. Because amphibians are extremely sensitive to environmental disturbances, understanding the factors that influence their development is essential for their conservation.

Conclusion

In summary, our study revealed that the chemical cues released by an Odonata predator affect both behavioral and morphological responses of larval anuran prey, suggesting that *R. diptycha* tadpoles exhibit functionally independent co-specialization in the expression of these two defensive phenotypes. Such coordinated expression of responses suggests that within and among habitat, predator avoidance by tadpoles operates simultaneously, where behavioral decisions enable short-term prey avoidance from predators and combined with morphological responses allow the exit of the aquatic environment through faster development.

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