Hydrobiologia (2019) 837:77–86
https://doi.org/10.1007/s10750-019-3962-3

PRIMARY RESEARCH PAPER

Space use and phenotypic plasticity in tadpoles under predation risk

Eduardo Oliveira Pacheco · Mauricio Almeida-Gomes · Diego José Santana · Rafael Dettogni Guariento

Received: 28 June 2018 / Revised: 9 April 2019 / Accepted: 19 April 2019 / Published online: 27 April 2019
© Springer Nature Switzerland AG 2019

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.

Keywords Foraging · Habitat avoidance · Ideal free distribution · Morphological plasticity · Patch choice

Handling editor: Lee B. Kats

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10750-019-3962-3) contains supplementary material, which is available to authorized users.

E. O. Pacheco (✉) · M. Almeida-Gomes · R. D. Guariento
Laboratório de Ecologia, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul Campo Grande, Cidade Universitária, 79002-970 Campo Grande, Mato Grosso do Sul, Brazil
e-mail: eduardopachecosd@gmail.com

D. J. Santana
Laboratório de Zoologia, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul Campo Grande, Cidade Universitária, 79002-970 Campo Grande, Mato Grosso do Sul, Brazil

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,

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

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

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

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

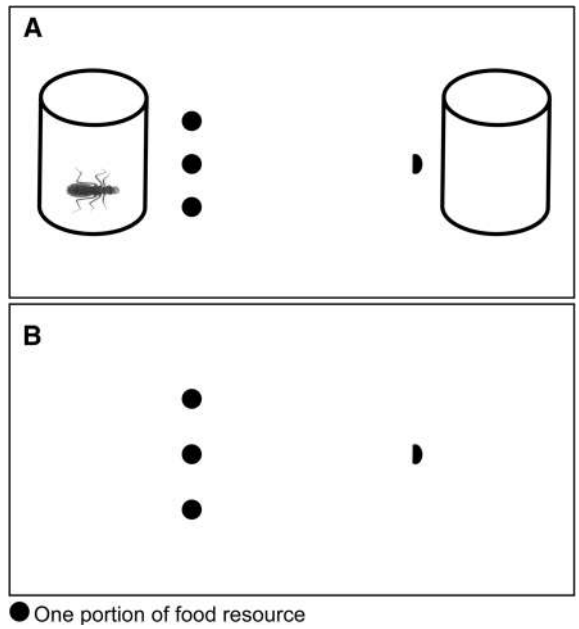

Fig. 1 Illustrative scheme of the experimental units. **A** Predation risk treatment ($N = 5$), with predator associated with the patch with abundant resources and **B** predator-free treatment ($N = 5$). The cage in the predation risk treatment had several small holes to permit the water flow inside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

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,

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

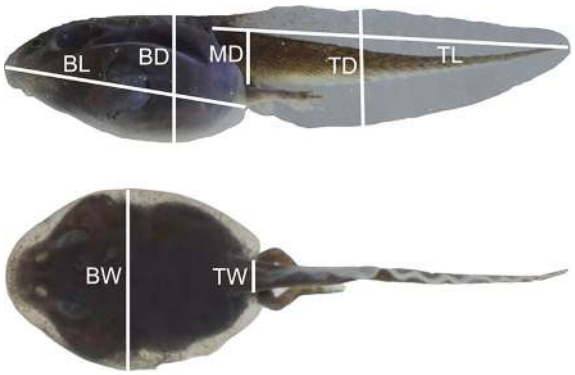

Fig. 2 Side view (above) and dorsal view (below) of a *Rhinella diptycha* tadpole illustrating the seven linear measures taken for morphological plasticity analysis (tail length—TL, tail depth—TD, body depth—BD, tail muscle depth—MD, body length—BL, tail width—TW, body width—BW). We used a tadpole at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

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

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 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.

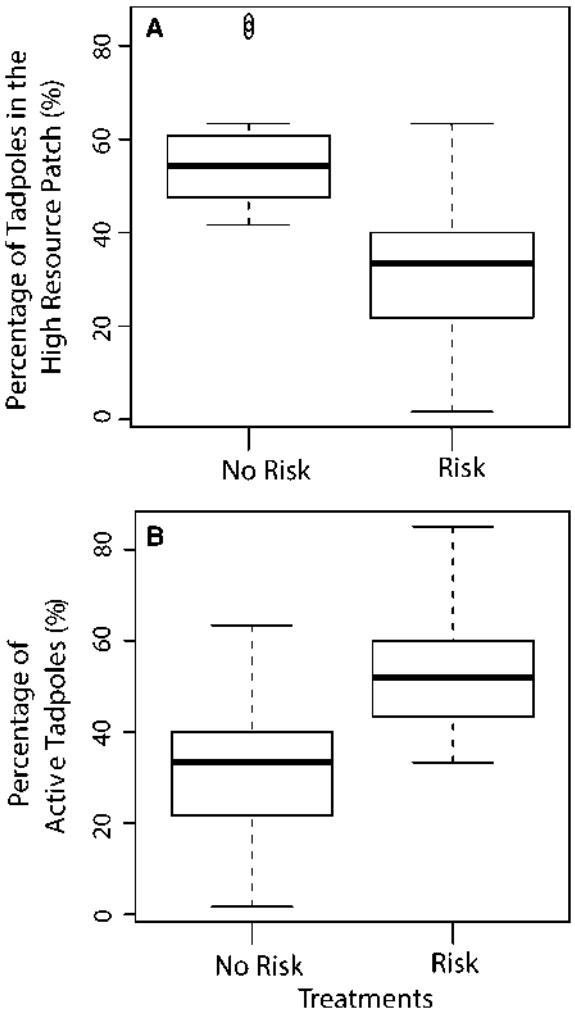

Fig. 3 **A** Box plot showing the mean and standard error of prey habitat use, where we observe that the use of high resource patch in risk treatment was higher than in control treatment. **B** Box plot showing the mean and standard error of tadpoles' activity between the treatments. Tadpoles exposed 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

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

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

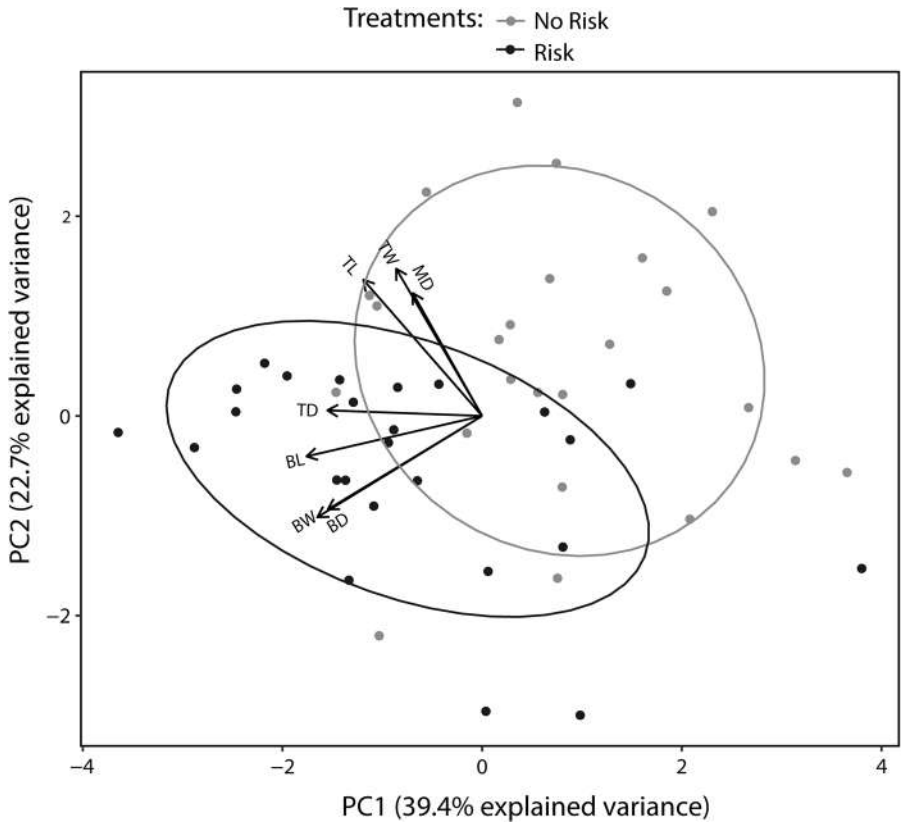

Fig. 4 Summary PCA biplot of the morphological data (tail length—TL, tail depth—TD, body depth—BD, tail muscle depth—MD, body length—BL, tail width—TW, body width—BW) among predation risk treatments

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 (Luttbeg & 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

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

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

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

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.

Acknowledgements We are grateful to Jefferson Medina, Nathalia Mangini, and Beatriz Carneiro for their support in field work and the montage of the experiment. We thank the Use Animal Ethics Committee from Federal University of Mato Grosso do Sul by the approval of this project (protocol#732/2015). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001. DJS thanks CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for his research fellowship (311492/2017-7). We also thank Dr. Luiz Gustavo de Oliveira-Santos for the helpful suggestions along the study.

References

Abrahams, M. & L. Dill, 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70: 999–1007.

Alonzo, S. H., 2002. State-dependent habitat selection games between predators and prey: the importance of behavioural interactions and expected lifetime reproductive success. Evolutionary Ecology Research 4: 759–778.

Anderson, R. B. & S. P. Lawler, 2016. Behavioral changes in tadpoles after multigenerational exposure to an invasive intraguild predator. Behavioral Ecology 27: 1790–1796.

Appleton, R. D. & R. A. Palmer, 1988. Water-borne stimuli released by predator crabs and damage prey induce more predator-resistant shells in a marine gastropod. Proceedings of the National Academy of Sciences 85: 4387–4391.

Bernot, R. J. & A. M. Turner, 2001. Predator identity and trait-mediated indirect effects in a littoral food web. Oecologia 129: 139–146.

Bookstein, F. L., 1997. Morphometric tools for landmark data: geometry and biology. Cambridge University Press, Cambridge.

Boyce, M. S., C. J. Johnson, E. H. Merrill, S. E. Nielsen, E. J. Solberg & B. Moorter, 2016. Can habitat selection predict abundance? Journal of Animal Ecology 85: 11–20.

Brown, J. S., B. P. Kotler & A. Bouskila, 2001. Ecology of fear: foraging games between predators and prey with pulsed resources. Annales Zoologici Fennici 38: 71–87.

Caldwell, G. S., 1986. Predation as a selective force on foraging herons: effects of plumage color and flocking. The Auk 103: 494–505.

Chivers, D. P. & R. J. F. Smith, 1998. Chemical alarm signalling in aquatic predator-prey systems: a review and prospectus. Ecoscience 5: 338–352.

Costello, D. M. & M. J. Michel, 2013. Predator-induced defenses in tadpoles confound body stoichiometry predictions of the general stress paradigm. Ecology 94: 2229–2236.

Crossland, M. R. & C. Azevedo-Ramos, 1999. Effects of *Bufo* (Anura: bufonidae) toxin on tadpoles from native and exotic *Bufo* habitats. Herpetologica 55: 192–199.

Davies, G. M. & A. Gray, 2015. Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). Ecology and Evolution 5: 5295–5304.

DeWitt, T. J. & R. B. Langerhans, 2003. Multiple prey traits, multiple predators: keys to understanding complex community dynamics. Journal of Sea Research 49: 143–145.

DeWitt, T. J., B. W. Robinson & D. S. Wilson, 2000. Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. Evolutionary Ecology Research 2: 129–148.

Edelaar, P., A. M. Siepielski & J. Clobert, 2008. Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. Evolution 62: 2462–2472.

Eklöv, P. & R. Svanbak, 2006. Predation risk influences adaptive morphological variation in fish populations. The American Naturalist 167: 440–452.

Ferguson, S. H., A. T. Bergerud & R. Ferguson, 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. Oecologia 76: 236–245.

Godin, J. & M. Keenleyside, 1984. Foraging on on patchily distributed prey by a cichlid fish (Teleosteicichlidae): a test of the ideal free distribution theory. Animal Behaviour 32: 120–131.

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

Gosner, K. L., 1960. A simplified table for staging anuran embryos larvae with notes on identification. Herpetologica 16: 183–190.
Gotceitas, V., 1990. Foraging and predator avoidance: a test of a patch choice model with juvenile bluegill sunfish. Oecologia 83: 346–351.
Guariento, R. D., B. Luttbeg, T. Mehner & F. A. Esteves, 2014. The effect of predation pressure and predator adaptive foraging on the relative importance of consumptive and non-consumptive predator net effects in a freshwater model system. Oikos 123: 705–713.
Guariento, R. D., B. Luttbeg, L. S. Carneiro & A. Caliman, 2018. Prey adaptive behaviour under predation risk modify stoichiometry predictions of predator-induced stress paradigms. Functional Ecology 32: 1631–1643.
Guariento, R. D., L. S. Carneiro, F. A. Esteves, J. S. Jorge & A. Caliman, 2015. Conspecific density affects predator-induced prey phenotypic plasticity. Ecosphere 6: 1–12.
Gunzburger, M. S. & J. Travis, 2004. Evaluating predation pressure on green treefrog larvae across a habitat gradient. Oecologia 140: 422–429.
Hammill, E. & A. P. Beckerman, 2010. Reciprocity in predator-prey interactions: exposure to defended prey and predation risk affects intermediate predator life history and morphology. Oecologia 163: 193–202.
Hammond, J. I., B. Luttbeg & A. Sih, 2007. Predator and prey space use: dragonflies and tadpoles in an interactive game. Ecology 88: 1525–1535.
Hanski, I. & O. Ovaskainen, 2000. The metapopulation capacity of a fragmented landscape. Nature 404: 755.
Heithaus, M. R. & L. M. Dill, 2002. Food availability and tiger shark predation risk. Ecology 83: 480–491.
Hero, J. M., W. E. Magnusson, C. F. Rocha & C. P. Catterall, 2001. Antipredator defenses influence the distribution of amphibian prey species in the central Amazon rain forest. Biotropica 33: 131–141.
Hossie, T., K. Landolt & D. L. Murray, 2017. Determinants and co-expression of anti-predator responses in amphibian tadpoles: a meta-analysis. Oikos 126: 173–184.
Howe, N. R. & Y. M. Sheikh, 1975. Anthopleurine: a sea anemone alarm pheromone. Science 189: 386–388.
Jara, F. G. & M. G. Perotti, 2010. Risk of predation and behavioural response in three anuran species: influence of tadpole size and predator type. Hydrobiologia 644: 313–324.
Kacelnik, A., J. R. Krebs & C. Bernstein, 1992. The ideal free distribution and predator-prey populations. Trends in Ecology & Evolution 7: 50–55.
Kerfoot, W. C., 1987. Translocation experiments: bosmina responses to copepod predation. Ecology 68: 596–610.
Kotler, B. P. & L. Blaustein, 1995. Titrating food and safety in a heterogenous environment: when are the risky and safety patches of equal value? Oikos 74: 251–258.
Krivan, V., 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. The American Naturalist 149: 164–178.
Krivan, V., 2003. Ideal free distributions when resources undergo population dynamics. Theoretical Population Biology 64: 25–38.
Lima, S. L., 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27: 215–290.
Lima, S. L. & L. M. Dill, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619–640.
Lima, S. L. & P. A. Bednekoff, 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. The American Naturalist 153: 649–659.
Luttbeg, B., J. I. Hammond & A. Sih, 2008. Dragonfly larvae and tadpole frog space use games in varied light conditions. Behavioral Ecology 20: 13–21.
Luttbeg, B. & A. Sih, 2004. Predator and prey habitat selection games: the effects of how prey balance foraging and predation risk. Israel Journal of Zoology 50: 233–254.
McCollum, S. A. & J. D. Leimberger, 1997. Predator-induced morphological changes in an amphibian: predation by dragonflies affects tadpole shape and color. Oecologia 109: 615–621.
McCoy, M. W., B. M. Bolker, C. W. Osenberg, B. G. Miner & J. R. Vonesh, 2006. Size correction: comparing morphological traits among populations and environments. Oecologia 148: 547–554.
McDiarmid, R. W. & R. Altig, 1999. Tadpoles: The Biology of Anuran Larvae. The University of Chicago Press, Chicago.
McIvor, C. C. & W. E. Odum, 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecology 69: 1341–1351.
Nomura, F., V. H. M. Prado, F. R. Silva, R. E. Borges, N. Y. N. Dias & D. D. C. Rossa-Feres, 2011. Are you experienced? Predator type and predator experience trade-offs in relation to tadpole mortality rates. Journal of Zoology 284: 144–150.
Pease, C. M., R. Lande & J. J. Bull, 1989. A model of population growth, dispersal and evolution in a changing environment. Ecology 70: 1657–1664.
Peckarsky, B. L., 1982. Aquatic insect predator-prey relations. BioScience 32: 261–266.
Perotti, M. G., L. A. Fitzgerald, L. Moreno & M. Pueta, 2006. Behavioral responses of *Bufo arenarum* tadpoles to odonate naiad predation. Herpetological Conservation and Biolology 1: 117–120.
Peterson, C. H. & G. A. Skilleter, 1994. Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica*, flow environment, and siphon-cropping fishes. Oecologia 100: 256–267.
Pigliucci, M., 2003. Phenotypic integration: studying the ecology and evolution of complex phenotypes. Ecology Letters 6: 265–272.
Pigliucci, M., 2005. Evolution of phenotypic plasticity: where are we going now? Trends in Ecology and Evolution 20: 481–486.
Prevedello, J. A., G. Forero-Medina & M. V. Vieira, 2010. Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. Journal of Animal Ecology 79: 1315–1323.
R Development Core Team, 2016. R: a langauge and environment for statistical coumputing. R Foundation for Statistical Computing, Vienna, Austria. http://R-project.org.
Ravigné, V., U. Dieckmann & I. Olivieri, 2009. Live where you thrive: joint evolution of habitat choice and local

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

adaptation facilitates specialization and promotes diversity. The American Naturalist 174: E141–E169.
Relyea, R. A., 2001. Morphological and behavioral plasticity of larval anurans in response to different predators. Ecology 82: 523–540.
Relyea, R. A. & J. T. Hoverman, 2003. The impact of larval predators and competitors on the morphology and fitness of juvenile treefrogs. Oecologia 134: 596–604.
Repka, S. & K. Pihlajamaa, 1996. Predator-induced phenotypic plasticity in *Daphnia pulex*: uncoupling morphological defenses and life history shifts. Hydrobiologia 339: 67–71.
Rodrigues, M. E. & F. O. Roque, 2017. Checklist de Odonata do estado de Mato Grosso do Sul, Brasil. Iheringia Série Zoologia 107: e2017117.
Schmidt, K. A., J. M. Earnhardt, J. S. Brown & R. D. Holt, 2000. Habitat selection under temporal heterogeneity: exorcizing the ghost of competition past. Ecology 81: 2622–2630.
Scrimgeour, G. J., J. M. Culp & F. J. Wrona, 1994. Feeding while avoiding predators: evidence for a size-specific trade-off by a lotic mayfly. Journal of the North American Benthological Society 13: 368–378.
Seebacher, F., C. R. White & C. E. Franklin, 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. Nature Climate Change 5: 61–66.
Shrader, A. M., G. I. H. Kerley, J. S. Brown & B. P. Kotler, 2012. Patch use in free-ranging goats: does a large mammalian herbivore forage like other central place foragers? Ethology 118: 967–974.
Skelly, D. K. & E. E. Werner, 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. Ecology 71: 2313–2322.
Souza, F. L., C. P. A. Prado, J. L. M. M. Sugai, V. L. Ferreira, C. Aoki, P. Landgref-Filho, C. Strüssmann, R. W. Ávila, D. J. Rodrigues, N. R. Albuquerque, J. Terra, M. Uetanabaro, A. F. Béda, L. Piatti, R. A. Kawashita-Ribeiro, M. Delatorre, G. F. Faggioni, S. D. B. Demczuk & S. Duleba, 2017. Diversidade de anfíbios do Estado de Mato Grosso do Sul, Brasil. Iheringia Série Zoologia 107: e2017152.
Stav, G., B. P. Kotler & L. Blaustein, 2007. Direct and indirect effects of dragonfly (*Anax imperator*) nymphs on green toad (*Bufo viridis*) tadpoles. Hydrobiologia 579: 85–93.
Takahara, T., H. Doi, Y. Kohmatsu & R. Yamaoka, 2013. Different chemical cues originating from a shared predator induce common defense responses in two prey species. Animal Cognition 16: 147–153.
Turkia, T., E. Korpimäki, A. Villers & V. Selonen, 2018. Predation risk landscape modifies flying and red squirrel nest site occupancy independently of habitat amount. PLoS ONE 13: e0194624.
Van Baalen, M. & M. W. Sabelis, 1993. Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. The American Naturalist 142: 646–670.
Van Buskirk, J. & M. Arioli, 2002. Dosage response of an induced defence: how sensitive are tadpoles to predation risk? Ecology 83: 1580–1585.
Van Buskirk, J., P. Anderwald, S. Lüpold, L. Reinhardt & H. Schuler, 2003. The lure effect, tadpole tail shape, and the target of dragonfly strikes. Journal of Herpetology 37: 420–424.
Van Buskirk, J., A. Krügel, J. Kunz, F. Miss & A. Stamm, 2014. The rate of degradation of chemical cues indicating predation risk: an experiment and review. Ethology 120: 942–949.
Wassersug, R. J., 1971. On the comparative palatability of some dry-season tadpoles from costa Rica. American Midland Naturalist 86: 101–109.
Wells, K. D., 2010. The Ecology and Behavior of Amphibians. University of Chicago Press, Chicago.
Werner, E. E., J. F. Gilliam, D. J. Hall & G. G. Mittelbach, 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540–1548.
Winandy, L., P. Legrand & M. Denoël, 2017. Habitat selection and reproduction of newts in networks of fish and fishless aquatic patches. Animal Behaviour 123: 107–115.
Wong, B. B. M. & U. Candolin, 2015. Behavioral responses to changing environments. Behavioral Ecology 26: 665–673.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Content courtesy of Springer Nature, terms of use apply. Rights reserved.

Terms and Conditions

Springer Nature journal content, brought to you courtesy of Springer Nature Customer Service Center GmbH (“Springer Nature”).
Springer Nature supports a reasonable amount of sharing of research papers by authors, subscribers and authorised users (“Users”), for small-scale personal, non-commercial use provided that all copyright, trade and service marks and other proprietary notices are maintained. By accessing, sharing, receiving or otherwise using the Springer Nature journal content you agree to these terms of use (“Terms”). For these purposes, Springer Nature considers academic use (by researchers and students) to be non-commercial.
These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the relevant terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). For Creative Commons-licensed articles, the terms of the Creative Commons license used will apply.
We collect and use personal data to provide access to the Springer Nature journal content. We may also use these personal data internally within ResearchGate and Springer Nature and as agreed share it, in an anonymised way, for purposes of tracking, analysis and reporting. We will not otherwise disclose your personal data outside the ResearchGate or the Springer Nature group of companies unless we have your permission as detailed in the Privacy Policy.
While Users may use the Springer Nature journal content for small scale, personal non-commercial use, it is important to note that Users may not:

1. use such content for the purpose of providing other users with access on a regular or large scale basis or as a means to circumvent access control;
2. use such content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval , sponsorship, or association unless explicitly agreed to by Springer Nature in writing;
4. use bots or other automated methods to access the content or redirect messages
5. override any security feature or exclusionary protocol; or
6. share the content in order to create substitute for Springer Nature products or services or a systematic database of Springer Nature journal content.

In line with the restriction against commercial use, Springer Nature does not permit the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Springer Nature journal content cannot be used for inter-library loans and librarians may not upload Springer Nature journal content on a large scale into their, or any other, institutional repository.
These terms of use are reviewed regularly and may be amended at any time. Springer Nature is not obligated to publish any information or content on this website and may remove it or features or functionality at our sole discretion, at any time with or without notice. Springer Nature may revoke this licence to you at any time and remove access to any copies of the Springer Nature journal content which have been saved.
To the fullest extent permitted by law, Springer Nature makes no warranties, representations or guarantees to Users, either express or implied with respect to the Springer nature journal content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.
Please note that these rights do not automatically extend to content, data or other material published by Springer Nature that may be licensed from third parties.
If you would like to use or distribute our Springer Nature journal content to a wider audience or on a regular basis or in any other manner not expressly permitted by these Terms, please contact Springer Nature at

onlineservice@springernature.com