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Temperature and predator cues shape antipredator behavior in Amazonian tadpoles

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Climate change has interfered with ecosystem stability, biodiversity and predator–prey interactions. Among amphibians, temperature variations may influence metabolism, sensory perception and behavior. We experimentally evaluated whether tadpoles of map treefrog, *Boana geographica*, reduce their activity and increase the use of refuge under different temperatures in response to chemical signals emitted by a predator, as an adaptive strategy to minimize the risk of predation. Tadpoles' shelter use and feeding behavior was measured at temperatures from 28 to 36 °C using control (without predator cues) and treatment (predator cues) groups. Temperature influenced the shelter use of tadpoles when exposed to predator chemical cues. Significant differences were observed at lower temperatures and greater shelter use by tadpoles at higher temperatures. Food offering showed no significant difference in the control or treatment group. The increased use of shelter by tadpoles in response to chemical signals from predators and increased temperature highlights the adaptive capacity of organisms in the face of predation threats, highlighting the complexity of predator–prey interactions. This behavior highlights the role of environmental factors and sensory signals in shaping the survival strategies of aquatic ectotherms. Tadpoles minimize predation risk by increasing predator avoidance behavior in detecting chemical signals in the water.

KEY WORDS: ecology of fear, climate change, trophic interactions, behavioral ecology, *Boana geographica*.

INTRODUCTION

Temperature is an important abiotic force shaping multiple processes in ecological communities like evolution, physiology, behavior, and trophic interactions. Temperature may increase the metabolic rates of both predators and prey, leading to more aggressive foraging behavior and altering the dynamics of predator–prey interactions (Barneche et al. 2017). The sensitivity of trophic interactions to temperature underscores the implications of climate change for ecosystem stability and

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biodiversity (Thackeray et al. 2016; Inagaki et al. 2020). As global temperatures continue to rise due to climate change, understanding the role of temperature in shaping trophic relationships becomes important for predicting and mitigating the impacts of environmental changes on communities. The effects of climate change may lead to population declines, reduced body size, fecundity and foraging, and changes in phenology and geographic distributions (Li et al. 2013; Radchuk et al. 2019; Domenici & Seebacher 2020).

Amphibians have permeable skin which can dry out easily, eggs with gelatinous shell, complex life cycles (for example, tadpoles require aquatic habitats and adults require terrestrial habitats) and are ectothermic, which makes them sensitive to changes in temperature and precipitation (Duellman & Trueb 1986). Growing research has examined global climate change's effects on amphibians since the increasing evidence of negative effects in such organisms (Li et al. 2013; Longhini et al. 2021; Luedtke et al. 2023). In ectothermic organisms such as amphibians, in addition to metabolic rates, temperature can affect sensory modalities critical for survival. Temperature influences the rate of chemical diffusion in water and, among many species, it also influences the physiological processes governing sensory perception, affecting the balance between prey survival and anti-predator behaviors (Troyer & Turner 2015; Hahn et al. 2020).

The map treefrog, *Boana geographica* Spix 1824, occurs in tropical South America east of the Andes. The species inhabit rainforests, and tadpoles are often found in streams and pools, where water is renewed. The tadpoles present a dark coloration and are aggregated in groups on the water column, forming large black masses that move in the water (Lima et al. 2005). Furthermore, map treefrog tadpoles display two main behavioral patterns: stationary and continuously moving (Caldwell 1989; Azevedo-Ramos et al. 1992). The stationary pattern has a thermoregulatory function, while the continuous movement pattern is preferred during tadpole grazing. In the stationary pattern, tadpoles stay in a single two-dimensional layer and alternate between periods of movement and stillness. As they move away, they swim back and head towards the center of the school and, in doing so, create a compact aggregation. The continuously moving pattern is three-dimensional, giving the appearance of something rolling slowly, and refers to the entire movement of the assembly (Caldwell 1989).

In this study, we investigated the behavior of map tree frog tadpoles along a range of temperatures to test the use of refuge in response to chemical signals released by a fish predator. We hypothesized that tadpoles reduce activity and increase the use of refuges as an adaptive strategy to minimize the risk of predation. Chemical perception between prey and predator plays an essential role in behavioral ecology. We expect tadpoles to respond to these danger signals by adjusting their behavior to increase the chances of survival in high-temperature environments where the risk of predation may be heightened.

MATERIAL AND METHODS

Seventy-two tadpoles of *B. geographica* were collected in a floodplain on 25 May 2023 at the Oriximiná municipality, State of Pará, Brazilian Amazonia (1.751955°S; 55.840466°W). After the capture, individuals were transported to the laboratory (10 min drive) in plastic bags. Individuals were transferred to a 50 L aquarium over 2 weeks in the laboratory for acclimation at

a temperature of 28 °C. The average size of the tadpoles was ~ 42 mm and the stage of development was 35 and 36 (sensu Gosner 1960).

Experimental design

The experiment was carried out between 12th and 21st June 2023. The tadpoles were equally distributed in six 50 L aquariums (width × length × height = 60 × 30 × 30 cm) containing 12 individuals each (Fig. 1). Each aquarium had a closed filtering system with biological, mechanical, and chemical filtering through a hang-on filter. The temperature was controlled through a digital thermostat (150 W). Physical-chemical parameters of the water (pH, NH₃, and NO₂) were measured daily to control the water characteristics. The tadpoles were kept on a 12/12 circadian cycle and fed once a day with granulated feed containing 29% protein.

The study was conducted using a control group and treatment group. The observations followed two stages: initially, the tadpoles were observed in the control group, without a predator. Next, the same 72 tadpoles were exposed to the presence of a predator, making up the treatment group. The experiment had 12 replicates, six for the control group and six for the treatment group. In the control group, tadpoles were exposed to temperature variation without the presence of a predator. In the treatment group, we added a fish predator, a small individual (average body size of 15 cm) of trahira, *Hoplias malabaricus* Bloch 1794, in each aquarium. The predators were conditioned on small cylindrical containers close to the water surface. The trahira and tadpoles were collected in the same place, at an ambient temperature of 28 °C. The predator container was pierced with small holes for water circulation. We wrapped the container with white non-toxic tape so there was no visual contact between the fish predator (trahira) and the prey (*B. geographica* tadpoles). The sides and back of the aquariums were covered with black paper to facilitate observation during the recordings and to minimize external interference. A brick was added to provide shelter, while the substrate at the bottom of the aquarium consisted of sand taken directly from the floodplain. In both the control and treatment groups, the tadpoles were exposed to a temperature gradient ranging from 28 to 36 °C, with a 1 °C increase in each temperature sampled. Two samples were taken at each temperature. The temperature range was determined based on the average annual temperature of the municipality of Oriximiná of 26 °C (Scoles et al. 2011) and the thermal tolerance range of the Hylidae family according to the literature (Brown 1969; Longhini et al. 2021).

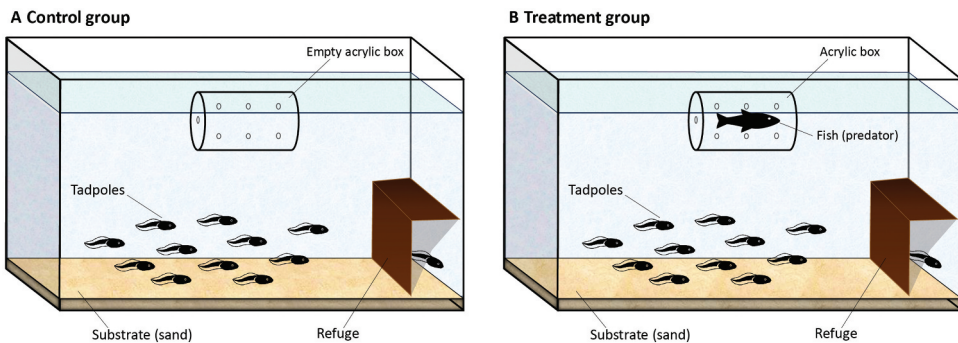


Fig. 1. — Experimental design. (A) Control group, without the predator's presence and with 12 tadpoles. (B) Treatment group, with the presence of the predator isolated in a cylinder.

Behavioral observation

Individuals were observed 4 times a day (9:00 am, 12:00, 3:00 and 5:30 pm), representing two temperature ranges (2 °C) sampled per day over 10 consecutive days (5 days predator absent and 5 days predator present), for all temperature ranges evaluated. Individuals were fed once a day (3:00 pm) and such information was added to the data as variable feeding. We analyze two behavioral patterns: shelter use and feeding. The behavior of tadpoles was recorded through 4 min video recordings through cameras positioned in front of each aquarium to avoid the potential bias of human presence in data collection. In the laboratory, we extracted frames from the last 5 sec of each minute from all videos and verified if tadpole individuals were exposed (outside the brick holes) or sheltered (inside the brick holes).

Ethical procedures

The experiment procedures were approved by the Animal Ethics Committee of Universidade Federal do Oeste do Pará (no. 0220230241). The specimen collection was conducted under permission of SISBIO (no. 88729-1). After the experiment, we euthanized all tadpoles and determined their development stages and total length.

Data analysis

A generalized linear model that accounted for repeated measures was fitted to test for the effects of chemical stimulus from fish predator in tadpole shelter use across temperatures. A one-way ANOVA was fitted to verify differences in the shelter use after the food offer. In both statistical tests, the dependent variable was square root transformed to meet normality. As there are many zeros in the data, before transforming them, the percentage data on the frequency of tadpoles in the treatment and control groups with a value of 0 were converted into 0.1 to meet with square root transformation assumptions (Zar 1999). Statistical analyses were conducted at a significance level of 0.05 using the R software v. 4.3.1 (R Development Core Team 2023).

RESULTS

There was a significant effect of the chemical cues of a fish predator on tadpole shelter use (mean \pm SE = 13.37 \pm 0.89% and 25.41 \pm 1.28% for control and treatment groups, respectively; Fig. 2A; Table 1). The use of shelter increased significantly between treatment and control groups and with rising temperatures. A higher frequency of shelter use was observed when predator cues were present. Temperature and the interaction between treatments significantly affected the use of shelter by the tadpoles. The most contrasting differences were observed in the lower temperature (28 °C) with tadpoles of the control group being more sheltered and from 33 °C onwards, tadpoles from the treatment group used more shelter than those from the control group (Fig. 2B). Sixty-nine percent of tadpoles from the treatment group were observed in the shelter at 36 °C. Feeding had a non-significant effect on control and treatment groups. Although tadpoles were less exposed to refuge in the treatment phase, an increase in the exposition was observed when individuals were fed in both control and treatment (Fig. 2C; Table 1). Nevertheless, we did not verify a significant difference in shelter use during the 4 min sampled after the feeding among control and treatment phases (Fig. 3).

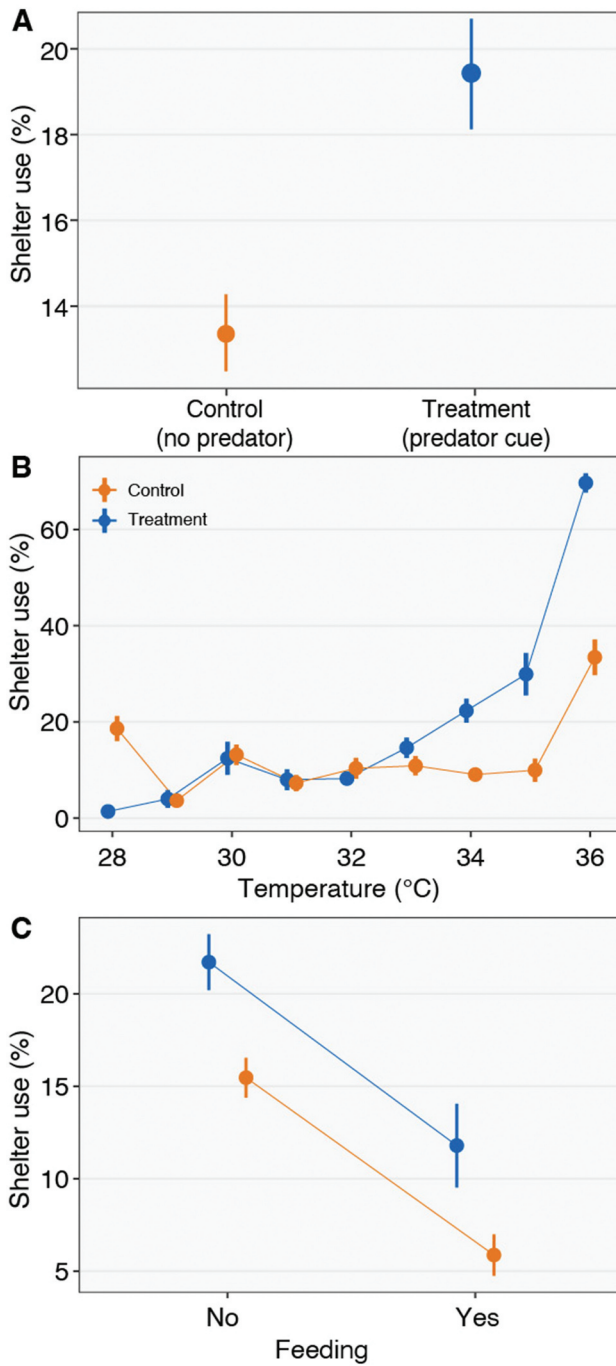


Fig. 2. — Patterns of shelter use in *Boana geographica* tadpoles with and without predator chemical cues (mean \pm SE values) according to (A) control vs treatment groups, (B) temperature and (C) feeding activity or not. See Table 1 for statistical results.

Table 1.

Outputs of the generalized linear model with repeated measures testing the effect of predator presence, temperature and its interaction in shelter use among *Boana geographica* tadpoles. Significant values are highlighted in bold.

Behavior	Factors	df	f	<i>P</i>
Shelter use	Predator	1	22.52	< 0.0001
	Temperature	8	67.06	< 0.0001
	Feeding	1	3.19	0.07
	Predator × Temperature	8	17.67	< 0.0001
	Predator × Feeding	1	0.28	0.59
	Temperature × Feeding	3	0.11	0.95
	Predator × Temperature × Feeding	3	2.25	0.08

df: degree of freedom, f: F test, *P*: statistical significance.

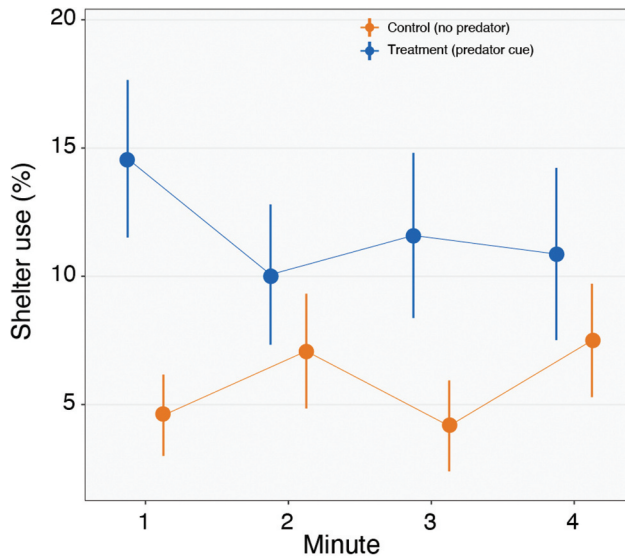


Fig. 3. — Patterns of shelter use (mean ± SE values) in *B. geographica* tadpoles during feeding activity at each minute sampled.

DISCUSSION

Our results revealed that temperature and predator chemical cues influence the behavior of Amazonian tadpoles. Such findings support our hypothesis that map treefrog tadpoles seek refuge with increasing temperatures in the presence of predators, showing greater sensitivity to the risk of predation between 33 and 36 °C.

Temperature variations may substantially influence sheltering behavior, possibly affecting predatory interactions and ecological dynamics (Gvoždík et al. 2021). The behavior of avoiding predators may be an energy-saving strategy to reduce vulnerability, considering that lethality increases from 35 °C for species of the Hylidae family (Turriago et al. 2015). This evidence highlights the importance of temperature in the response of tadpoles to imminent risk from predators and how environmental attributes influence the behavior and survival of this species.

To assess the risk of predation, amphibian larvae generally rely on chemical signals transmitted by the water (Scarabotti et al. 2007). The chemical substances to which prey respond can be predator-specific odors, signals released by members of the same species, or, more often, a combination of the two (Chivers & Smith 1998; Fraker 2009; Schoeppner & Relyea 2009; Hetttyey et al. 2010). In natural environments, tadpoles may live under great predation pressure. Such pressure results in the evolution of defense mechanisms to escape predation and promote survival (Schmidt & Amézquita 2001). An important issue addressed in this study concerns the mechanism by which tadpoles detect the predator; many prey can detect specific odors and react adaptively by activating defense mechanisms, such as fleeing, hiding or camouflaging themselves. Anurans show a variety of behaviors, from remaining static to extreme flight, indicating a dangerous situation (Kiesecker et al. 1996; Williams et al. 2000; Toledo et al. 2007). Predators often use chemical signals to identify their prey, identify partners or defend territory (Toledo et al. 2011). Thus, the evolution of these chemical communication strategies is often shaped by the selective pressure of predator–prey interactions, which contributes to the adaptation and maintenance of the species involved.

The observed higher use of shelter among tadpoles exposed to chemical cues from the predators and increasing temperature underlines the adaptive responses of organisms in response to predation threats, highlighting the dynamic nature of predator–prey interactions. This observation aligns with the risk allocation hypothesis, suggesting that prey organisms modulate their behavior based on perceived risk levels (Lima & Bednekoff 1999; Ferrari et al. 2009). The exposure to predator olfactory cues may reduce locomotion activities in vertebrate and invertebrate prey taxa (Bourdeau & Johansson 2012).

Control and treatment groups showed greater exposure during the feeding period. This behavior is probably related to the trade-off between the cost of predator exposure by foraging and the energetic gains resulting from it, given that in a scenario of rising temperatures the individuals preferred to invest in energetic gains, even at the cost of an increased risk of predation (Schiwitz et al. 2020). Limited foraging could lead to further consequences, such as inadequate metamorphosis and negative effects in the adult stage (Bridges 2002). In general, this choice may have influenced foraging time, since there was no significant difference in shelter use during feeding, and the individuals were not inhibited by being more exposed. Such behavior may be mediated by the social foraging behavior, where individuals seek and search for food in groups, analyzing the benefits and tradeoffs of collective searching and feeding behaviors regarding efficiency, competition, and predator detection (Araújo & Lopes 2011). In addition, the conditioning of the tadpoles to offer a single food may have led to this result and to group foraging behavior since, with increased temperature, the metabolism tends to accelerate to meet the need for food sources. An increase in temperature, even for short periods, is enough to increase the metabolic activity of tadpoles and speed up their development, but also to reduce their survival (Gómez 2023).

Our study revealed that both temperature and the chemical cues of predators influence the predator avoidance behavior of Amazonian tadpoles. Tadpoles were sheltered at a higher frequency when exposed to predator chemical cues than when a predator was absent. This behavior underscores the role of environmental factors and sensory cues in shaping the survival strategies of aquatic ectotherms. Tadpoles minimize predation risk by increasing predator avoidance behavior in the presence of chemical signals in the water, highlighting the interaction between temperature, chemical signaling and predator-prey dynamics. Our results contribute to understanding the effects of climate change on trophic interactions.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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ETHICAL STANDARD

This project and manuscript meet institutional and professional ethical standards.

AUTHOR CONTRIBUTION

A. Albuquerque and D. Marinho: study design, statistical analysis, data collection and manuscript writing; J.V. Pinheiro and D.P. De Castro: study design and manuscript writing, C. S. Narciso: statistical analysis. V.J. Giglio: study design, statistical analysis, manuscript writing and funding. A. Albuquerque and D. Marinho contributed equally to this work and share first authorship.

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