



# Perception of con- and heterospecific injury cues in tadpoles of dendrobatid, ranid and bufonid frogs (Anura)

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## Abstract

Predator-prey interactions are vital for organismal survival. They shape anti-predator mechanisms and often depend on sensory abilities. Tadpoles use chemical cues, such as injury cues (alarm cues), to assess predation risks and modify their life-history, morphology, and behaviours accordingly. However, the prevalence of chemically mediated anti-predator responses in species with distinct ecological niches (e.g. within phytotelmata) remains unknown, hindering our understanding of the ecological significance and evolution of alarm substances. Therefore, our study aimed to investigate chemically mediated anti-predator responses in tadpoles of two Neotropical poison dart frogs, *Ranitomeya sirensis* and *Epipedobates anthonyi* (and compare their responses to two Palearctic model organisms, *Rana temporaria* and *Bufo bufo*, which are known to utilise alarm substances). Through behavioural bioassays, we exposed predator-naïve tadpoles to extracts of each species (i.e. con- and heterospecific cues), including water as a control (i.e. five treatments per species). We assessed changes in their activity before and after stimulus introduction. Our results show that *E. anthonyi* did not respond to any of the stimuli, whereas *R. sirensis* displayed increased activity levels exclusively in response to conspecific cues, but not to heterospecific cues. With this, our findings suggest a specialized recognition system in *R. sirensis*, potentially directed at conspecific competitors but likely unrelated to anti-predator mechanisms. In contrast, *E. anthonyi* may be insensitive to injury cues or utilize alternative sensory modalities to respond to acute predation events. This study sheds light on the chemical alarm response system of Neotropical poison dart frog tadpoles, providing foundational understanding of how dendrobatids react to injury cues. It prompts questions about the ecological significance and evolutionary implications of chemical communication in species facing extreme resource limitation during development and underscores the importance of comparative research for understanding chemical communication in diverse aquatic ecosystems.

**Keywords** Dendrobatidae · Chemical communication · Anti-predator · Behaviour · Alarm substance · Damage-released alarm cue

## Introduction

Predation plays a crucial role in the survival of organisms, driving the evolution of sophisticated sensory abilities and plastic anti-predator mechanisms (Ferrari et al. 2010; Bradbury and Vehrencamp 2011; Davies et al. 2012). Olfaction plays a critical role in evading predation, especially in aquatic ecosystems, where other sensory modalities are limited or impaired (Ferrari et al. 2010; Bradbury and Vehrencamp 2011). Thus, aquatic prey organisms heavily rely on chemical cues to evaluate and efficiently respond to ambient predation risks (Kats and Dill 1998; Ferrari et al. 2010; Brönmark and Hansson 2012). Chemical cues from conspecifics and predators, in particular, provide valuable information about spatial and temporal predation risks (Kats and Dill 1998; van Buskirk and Arioli 2002; Ferrari et al. 2006; van Buskirk et al. 2014; Crane et al. 2023) as well as predator identity (Relyea 2003; Hawkins et al. 2007), enabling prey to regulate their short-term defences in a threat-, context- and species-dependent manner (Ferrari et al. 2010; Hossie et al. 2016; Mitchell et al. 2017). With this, accurate identification of chemical cues is imperative for survival and leads to the evolution of both innate (Petranka and Hayes 1998; Fendt 2006; Epp and Gabor 2008; Lau et al. 2021) and acquired cue identification (i.e. learning processes; Suboski 1990; Mirza and Chivers 2000; Dalesman et al. 2006; Mirza et al. 2006; Ferrari et al. 2010).

Amphibian larvae, due to their aquatic lifestyle and heightened vulnerability during early developmental stages (Duellman and Trueb 1994; McDiarmid and Altig 1999; Wells 2007), have evolved anti-predator mechanisms centred around the perception of predator- and prey-borne cues (Ferrari et al. 2010; Hettyey et al. 2015; Hossie et al. 2016; Mitchell et al. 2017). Tadpoles use predator kairomones (predator odours and diet cues; Mitchell et al. 2017) but also prey-borne cues emitted by stressed or injured conspecifics (disturbance cues or injury cues; Mitchell et al. 2017; see also Caballero-Díaz et al. 2023 for the use of social cues) to assess ambient predation risk. They use these cues to respond by altering morphology (van Buskirk and Mccollum 2000; Relyea 2001; Teplitsky et al. 2005; Hossie et al. 2010; Middlemis Maher et al. 2013) life-history (Chivers et al. 2001; Relyea and Auld 2004; Ireland et al. 2007; Gazzola et al. 2015), and behaviour (van Buskirk and Mccollum 2000; Relyea 2001; Ferrari et al. 2009a; Fraker et al. 2009; Hossie et al. 2010; Rödin-Mörch et al. 2011; Gazzola et al. 2015; Hettyey et al. 2015; Bairos-Novak et al. 2020). Behavioural response patterns towards prey-borne injury cues tend to emerge at the family level (Rödin-Mörch et al. 2011). For example, bufonid tadpoles predominantly display avoidance and vivacity upon perceiving conspecific injury cues, whereas ranid tadpoles exhibit a broader spectrum of behavioural responses, including reduced activity and avoidance (Rödin-Mörch et al. 2011). Although the study of chemical communication and anti-predator responses in tadpoles has gained significant attention (Schulte et al. 2023), there is still a notable gap in our understanding, particularly regarding species with specific ecological niches and environmental interactions.

Previous research has primarily focused on a few anuran families, predominantly studying species with high larval individual counts and gregarious tendencies (e.g. loose association and shoaling behaviour with kin or conspecifics; Rödin-Mörch et al. 2011; Hossie et al. 2016). This limited focus excludes families or species characterised by low larval individual counts, non-social behaviours (including latent aggression towards conspecifics), or habitats with extreme resource limitations (i.e. space and food availability) which are equally important to comprehensively understand chemical communication systems and alarm sub-

stance evolution in tadpoles (Summey and Mathis 1998; Chivers et al. 2012). Among these understudied groups, the Neotropical poison dart frogs (Dendrobatidae and Aromobatidae; Grant et al. 2006) offer intriguing prospects for investigating the ecological and evolutionary significance of alarm cues and chemically mediated anti-predator responses.

Neotropical poison dart frogs primarily inhabit the tropical rainforests of Central and South America (Lötters et al. 2007) and are renowned for their aposematic skin colouration, which deter predators and signal their toxicity (Maan and Cummings 2012; Saporito et al. 2012). In addition they exhibit complex parental care behaviours, including egg attendance, tadpole transport, and offspring provisioning (Summers and Tumulty 2014; Schulte et al. 2020; Schulte and Summers 2021). The tadpoles of many species rely on specific larval deposition habitats, such as phytotelmata, which are small water reservoirs in leaf axils, bromeliad pools, or water-filled cavities in trees (Brust 1993; Caldwell and De Araújo 1998; Summers 1999; Poelman and Dicke 2007; Wells 2007). This habitat and corresponding lifestyle (i.e. solitary or small groups) is in stark contrast to that of typical model organisms, most notably from the families Ranidae and Bufonidae, with distinctly larger clutch sizes, high degree of larval sociality and ecological interactions (Duellman and Trueb 1994; Wells 2007). While evidence suggests poison dart frog tadpoles are able to assess and respond to visual predator cues (i.e. predator presence; Stynoski and Noble 2012; Szabo et al. 2021) and potentially kairomones (Szabo et al. 2021), the prevalence and significance of chemically mediated anti-predator responses among Neotropical poison dart frog tadpoles remains unknown. Given the unique ecological characteristics and complex life history of Neotropical poison dart frogs, investigating the presence and effectiveness of chemically mediated anti-predator responses in their tadpoles can greatly contribute to our understanding of the evolution and adaptive significance of alarm substances in poison dart frog tadpoles and other anuran taxa (Summey and Mathis 1998; Hagman 2008; Chivers et al. 2012; Wisenden 2015).

In this comparative study, we primarily aimed to expand and investigate chemically mediated anti-predator behaviour in response to conspecific injury cues (i.e. prey-borne chemical cues that indicate acute predation events like predator attacks or capture of prey; Hettyey et al. 2015; Wisenden 2015) in poison dart frogs. Specifically, we focused on two Neotropical poison dart frogs of the family Dendrobatidae, *Ranitomeya sirensis* and *Epipedobates anthonyi*. While *R. sirensis* lays 2–4 eggs and transports their predatory (potentially cannibalistic) tadpoles individually into small phytotelmata (e.g. bromeliad leaf axils; Brown et al. 2011; Kahn et al. 2016), *E. anthonyi* lays 5–32 eggs and transports their tadpoles in groups into small streams, puddles or water-filled holes in boulders (Lötters et al. 2007). Unlike *R. sirensis*, tadpoles of *E. anthonyi* do not show aggressive behaviours towards other tadpoles (Walls 1994). Furthermore, we sought to compare the response (changes in activity) to conspecific injury cues of these two species with two commonly studied model organisms (within the context of chemical communication): *Rana temporaria* (Ranidae) and *Bufo bufo* (Bufonidae). Both species lay clutches of several thousand eggs in temporal and permanent ponds (Lardner 2000; Glandt 2018), and the resulting tadpoles exhibit aggregations characterised by non-aggressive behaviour towards each other (Wells 2007). In addition to our main goal, we sought to contribute to the understanding of the evolutionary and ecological significance of these substances in tadpoles by exploring the responses of all species involved to all possible heterospecific injury cues. Considering cross-species reactions and phylogenetic differences (especially concerning *R. temporaria* and *B. bufo*)

helps refine hypotheses and develop future studies about the evolution of injury cues, their characteristics (i.e. phylogenetically conserved and/or convergent elements), and ecological significance (Summey and Mathis 1998; Hagman 2008; Chivers et al. 2012; Wisenden 2015).

We predict that (Hy1) *Ranitomeya sirensis* tadpoles will show no behavioural changes in response to both con- and heterospecific injury cues, reflecting absent evolutionary adaptations to discern and interpret these cues as heightened predation risk, given their solitary lifestyle, cannibalistic tendencies and limited options for action in their resource-limited environment (i.e. small water bodies in bromeliad leaf axis). We further predict that (Hy2) *Epipedobates anthonyi*, tadpoles will show decreased levels of activity in response to conspecific injury cues, reflecting evolutionary adaptations to enhance fitness by discerning and interpreting conspecific injury cues as heightened predation risks by sit-and-wait predators (Greeney 2001; McKeon and Summers 2013), facilitated by their gregarious lifestyle (i.e. loose aggregation with conspecifics and kin) in resource limited environments (e.g. small puddles or water-filled holes in boulders). Furthermore, we expect the strongest response (decrease in activity) towards conspecific injury cues and diminished anti-predator behaviour towards heterospecific injury cues, attributable to phylogenetic differences. Lastly, previous studies indicate that both *Rana temporaria* and *Bufo bufo* exhibit reduced activity levels as typical anti-predator responses to various predators (Van Buskirk 2001; Marquis et al. 2004; Maag et al. 2012; Nunes et al. 2013). Therefore, we predict that (Hy3a) *R. temporaria* and (Hy3b) *B. bufo* tadpoles will show reduced activity levels in response to conspecific injury cues and diminished anti-predator responses towards heterospecific injury cues, attributable to phylogenetic differences.

## Methods

### Animals

*Ranitomeya sirensis* (Aichinger, 1991) is a dendrobatid species endemic to the Serranía de Sira mountain range in east-central Peru (Lötters et al. 2007). *Epipedobates anthonyi* (Noble, 1921) occurs in southwestern Ecuador and northwestern Peru, extending west of the Andes at elevations ranging from 153–1387 m (Lötters et al. 2007). Tadpoles of *R. sirensis* and *E. anthonyi* used in this study were obtained from laboratory populations maintained at the Goethe University in Frankfurt am Main since 2018 (see supplementary material S1 for husbandry of adults). In laboratory populations, adult poison dart frogs deposited tadpoles in 50 mL falcon tubes or 280 mL beakers, which we then removed regularly and transferred to a dedicated tadpole housing environment. Newly hatched *R. sirensis* tadpoles were transferred into separate housing beakers individually (8.5 cm diameter, water level 4 cm), while *E. anthonyi* tadpoles were placed in tanks as sibling groups of 10 to 20 individuals (30×20 cm, water level 7 cm). Both tadpole housing environments were filled with demineralised water and included pieces of dried almond leaves (*Prunus dulcis*). Tadpoles of *Rana temporaria* (Linnaeus, 1758) and *Bufo bufo* (Linnaeus, 1758) were obtained by collecting and culturing eggs from a wild population where both species occur sympatrically. We collected eggs from 12 clutches annually (in each breeding season) from a permanent pond built by the Naturschutzbund Deutschland (NABU) in Steinau-Marborn, Hesse, Ger-

many (coordinates: 50°19'34.28" N, 9°25'27.08" E). The eggs were transferred to cooling boxes with water from the collection site and transported within 1 h to the animal maintenance facilities at Goethe University of Frankfurt. In the laboratory, the eggs hatched, and the tadpoles were reared in large glass aquaria (40×50×100 cm) containing 200 L of well-aerated aged tap water (1–2 individual's/L). The tanks were equipped with an air lift pump, sponge ceramic rings filter system and enriched with synthetic algae, clay pots, and stones to provide hiding places for the tadpoles. Months in advance, the filter system and water were inoculated with bacteria, phyto- and zooplankton from the respective collection sites.

Individuals of all species (breeding adults and tadpoles alike) were kept in the same room at constant temperatures (23–25 °C) and 12 L:12D photoperiod. Tadpoles of all species were fed with nettle powder every 2nd day and occasionally supplemented with rabbit chow. Water changes (25–50%) for tadpoles of *R. temporaria* and *B. bufo* were performed every third day, whereas tadpoles of *R. sirensis* and *E. anthonyi* did not require any water changes.

## Behavioural assay

To investigate tadpole responses to conspecific and heterospecific injury cues, we conducted a series of behavioural bioassays between April 2021 and May 2023. The bioassays involved investigating the activity of predator-naïve tadpoles from *Ranitomeya sirensis* ( $N=140$ ), *Epipedobates anthonyi* ( $N=141$ ), *Rana temporaria* ( $N=134$ ) and *Bufo bufo* ( $N=135$ ), before and after the introduction of one of five different stimuli (i.e. five treatments). In each trial, tadpoles were individually placed in plastic cups (8 cm in diameter) filled with 495 mL of water and exposed to extracts of either *R. sirensis* (x-Rs), *E. anthonyi* (x-Ea), *R. temporaria* (x-Rt), *B. bufo* (x-Bb) or water (control). Thus, tadpoles of every species were exposed to (a) conspecific extracts, (b) each of one of three possible heterospecific extracts and (c) water as a control. Each trial comprised three phases: (1) pre-stimulus, (2) stimulus, and (3) post-stimulus (each lasting 5 min). After an acclimatisation period (1 h) the trials started with the pre-stimulus phase, followed by the administration of one of the five stimuli mentioned. To introduce the stimuli, we gently placed the syringes on the cups' side without disturbing the animal. We then slowly dripped the content (5mL) into the cups, which marked the start of the stimulus phase. Prior observations (test with food dye) ensured 5 min time to be adequate for the stimulus to disperse in the second phase throughout the entire water body before initiating the post-stimulus phase; upon completion, a trial ended. Tadpole activity was recorded during the trials using a Panasonic camera and a mirror positioned at a suitable angle over the cups to capture the cups interior without obstructing the camera's line of sight. Observer presence was found to have no impact on tadpole activity based on preliminary trials (see also McIntyre et al. 2004; Carlson et al. 2015). Therefore, we carefully stepped in front of the sides of the mirror to apply the stimuli via the syringes. To minimise a potential influence of "time-of-day effects" on tadpole behaviour (e.g. Ferrari et al. 2008b), the trials were conducted alternately at one of five different time slots between 10:00 and 17:00 each day. Moreover, we ensured that the same species-stimulus combination was not tested on two consecutive days during the same time slot. Each individual underwent a single testing session. The specific developmental stages of tadpoles in bioassays according to Gosner (1960), were: *R. sirensis* (28–36), *E. anthonyi* (28–36), *R. temporaria* (28–32), and *B. bufo* (28–32).

## Extraction of injury cues

To obtain injury cues indicating acute predatory events (Hettley et al. 2015; Wisenden 2015), we randomly selected tadpoles from husbandry environments and euthanised them with a blow to the head (Ferrari et al. 2007; Lucon-Xiccato 2019a,b). This physical method was chosen to preserve the activity of alarm substances, as previous studies have shown negative effects of chemical euthanasia methods (i.e. anaesthetics) on alarm substance activity in fish (Losey and Hugie 1994) and tadpoles (Achtymichuk et al. 2022; own unpublished data). Moreover, we prepared extracts immediately before each trial (within 30 min of euthanasia) to avoid the degradation of substances mediating anti-predatory responses (van Buskirk et al. 2014; Crane et al. 2023). Euthanised tadpoles were pooled and homogenised in 2 ml of water using a handheld rotor-stator homogeniser (TissueRuptor II, Qiagen). The crude extracts were then centrifuged (10,000 ×g for 10 min at 4 °C) to separate water-soluble from insoluble fractions. The aqueous supernatant was diluted with water (5mL per euthanised tadpole), split up and loaded into 5mL syringes, and used immediately in the bioassay. The choice of water type for extract preparation (demineralised or aged tap-water) depended on the species used in the bioassay due to differences in the husbandry of tadpoles. Demineralised water was used for bioassays with dendrobatid tadpoles, while aged tap-water was used for bioassays with ranid and bufonid tadpoles. Given the lack of available information regarding the dose-dependent effects of alarm substances in poison dart frogs, we opted for sacrificing one tadpole per individual participating in the bioassay (tadpoles euthanized: *Ranitomeya sirensis* ( $N=140$ ), *Epipedobates anthonyi* ( $N=141$ ), *Rana temporaria* ( $N=134$ ) and *Bufo bufo* ( $N=135$ )). This approach allowed us to obtain preliminary insights into the perception of alarm substances in poison dart frog tadpoles within an anti-predator context, while also ensuring comparability between species in this study. To record the applied biomass in bioassays but reduce handling of animals, we conducted regular weight measurements of participating tadpoles every 3rd day. For this, we used a microscale and a small beaker with a specific volume of water to introduce the tadpoles, and then calculated the differences to determine the wet biomass of tadpoles used for extract preparation. The final concentrations of extracts per trial were as follows: x-Rs (0.20–0.48 mg/mL), x-Ea (0.28–0.64 mg/mL), x-Rt (0.11–0.44 mg/mL), and x-Bb (0.09–0.38 mg/mL). With this, the applied end concentrations were above concentrations used in studies with evident responses from ranid and bufonid tadpoles (e.g. Hagman and Shine 2008; Fraker et al. 2009; Lucon-Xiccato 2019a,b; Crossland et al. 2019). The specific developmental stages of the tadpoles used for extract preparation, according to Gosner (1960), were: *R. sirensis* (28–38), *E. anthonyi* (28–38), *R. temporaria* (28–32), and *B. bufo* (28–32).

## Video evaluation and statistical analysis

To compare the recorded tadpole behaviour before and after stimulus application, we quantified tadpole activity (total time being active) in the (1) pre- and (3) post-stimulus phases by scoring their total active time (in seconds) using the behaviour coding software “Cow-Log.” (Version 3.0.2; Hänninen and Pastell 2009). Tadpoles were considered active when moving (i.e. swimming or exhibiting tail movement). Tadpoles showing slight tail movements that did not result in forward body movement were also considered active, as dendrobatid tadpoles often inhabit spatially limited environments (Brust 1993; Caldwell and

De Araújo 1998; Summers 1999; Poelman and Dicke 2007). We then calculated a response index (response activity) for each individual within a treatment as the difference between the activity in the (3) post- and (1) pre-stimulus phase: [post - pre=response activity]. Therefore, the response activity represented the change in activity following exposure to the stimuli in phase (2), with positive numbers indicating increases and negative numbers indicating decreases in activity. Animals that had been inactive in both phases were excluded from the analysis. Due to data non-normality (assessed by the Kolmogorov-Smirnov test), tadpole responses of each species were compared using a Kruskal-Wallis one-way ANOVA (k samples). The dependent variable was “response activity” and the groups included in the analysis were “treatments” (i.e. five stimuli tested). Significant test results of species were subsequently assessed using Mann-Whitney U pairwise comparisons of each extract (x-Rs, x-Ea, x-Rt, x-Bb) against the control (water), including a Bonferroni-adjusted alpha value for four comparisons ( $P=0.0125$ ). Each species was analysed individually (i.e. no statistical analysis of treatments between species). All statistical analyses were conducted using SPSS 20 (SPSS Inc., Chicago, IL, USA).

## Results

We quantified the activity and calculated the median response activity for tadpoles of *Ranitomeya sirensis* ( $N=129$ ), *Epipedobates anthonyi* ( $N=131$ ), *Rana temporaria* ( $N=131$ ) and *Bufo bufo* ( $N=135$ ; Table 1). Kruskal-Wallis one-way ANOVA rejected the null hypothesis for *R. sirensis* ( $H=9.532$ ,  $df=4$ ,  $P<0.05$ ), *R. temporaria* ( $H=29.989$ ,  $df=4$ ,  $P<0.0001$ ) and *B. bufo* ( $H=9.703$ ,  $df=4$ ,  $P<0.05$ ), indicating significant differences between tadpole responses towards introduced stimuli. Kruskal-Wallis test, however, did not reject the null hypothesis for tadpole responses of *E. anthonyi* ( $H=3.527$ ,  $df=4$ ,  $P=0.474$ ), indicating no significant differences towards any of the introduced stimuli. Therefore, Mann-Whitney U post hoc tests were conducted to compare response activities among treatments for *R. sirensis*, *R. temporaria*, and *B. bufo* (Table 2).

In *R. sirensis* a significant difference in tadpole activity was observed between the control and the group exposed to x-Rs ( $Z = -2.587$ ,  $P=0.010$ ). Tadpoles exposed to extracts of conspecifics exhibited higher median response activity than the control, indicating increased activity (Table 1; Fig. 1). No significant difference in *R. sirensis* tadpole activity was observed between the control group and those exposed to heterospecific extracts (x-Ea, x-Rs, and x-Bb).

In *R. temporaria*, significant differences were found in tadpole activity between the control and the groups exposed to x-Rs ( $Z = -3.086$ ,  $P=0.002$ ), x-Ea ( $Z = -2.848$ ,  $P=0.004$ ) and x-Rt ( $Z = -4.731$ ,  $P<0.001$ ). Tadpoles exposed to extracts of conspecifics, as well as heterospecific extracts of both poison dart frog species (*R. sirensis*, *E. anthonyi*) showed decreased median response activity compared to the control group, indicating reduced activity. No significant difference in *R. temporaria* tadpole activity was found between the control and the group exposed to x-Bb.

In *B. bufo* a significant difference in tadpole activity was observed between the control group and the group exposed to x-Rt ( $Z = -2.989$ ,  $P=0.004$ ). Tadpoles exposed to heterospecific *R. temporaria* extracts exhibited higher median response activity than the control group, indicating increased activity. No significant difference in *B. bufo* tadpole activity was

**Table 1** Median response activities for tadpoles of four anuran species after experiencing different stimuli in five treatments. Positive values represent an increase, negative numbers a decrease in activity in the post-stimulus phase compared to the pre-stimulus phase

Treatment	<i>Ranitomeya sirensis</i>				<i>Epipedobates anthonyi</i>				<i>Rana temporaria</i>				<i>Bufo bufo</i>			
	N	Median	IQR	[75%]	N	Median	IQR	[75%]	N	Median	IQR	[75%]	N	Median	IQR	[75%]
Control	38	0.29	-4.55	9.43	43	-2.08	-8.94	6.90	29	-4.79	-13.72	10.68	30	-2.59	-6.63	9.28
x-Rs	24	19.73	-9.16	33.21	22	-5.11	-10.87	3.61	23	-17.39	-40.42	-8.69	25	-2.88	-27.90	27.46
x-Ea	21	10.73	-6.59	21.82	22	.090	-6.69	6.45	20	-22.69	-40.18	-8.20	20	2.38	-16.86	23.87
x-Rt	23	-0.22	-10.49	14.80	22	-4.35	-16.08	1.11	30	-27.98	-51.53	-16.89	30	19.72	-1.57	34.65
x-Bb	23	9.48	-4.20	31.62	22	-3.32	-26.65	7.28	29	-12.29	-18.02	-4.07	30	-0.17	-12.28	16.86

Stimulus types used in treatments: Control=water, x-Rs=*R. sirensis* extract, x-Ea=*E. anthonyi* extract, x-Rt=*R. temporaria* extract, x-Bb=*B. bufo* extract



**Table 2** Mann-Whitney-U post hoc comparisons of tadpole response activities (dependent variable) between treatments, following significant Kruskal-Wallis one-way ANOVA test results for *Ranitomeya sirenisis* (N=129), *Rana temporaria* (N=131), and *Bufo bufo* (N=135). Bold type indicates significant differences after Bonferroni adjusted alpha level for four comparisons (P=0.0125). Kruskal-Wallis one-way ANOVA did not reveal significant differences for *Epipedobates anthonyi* bioassays

Treatment	<i>Ranitomeya sirenisis</i>		<i>Rana temporaria</i>		<i>Bufo bufo</i>	
	Z	P	Z	P	Z	P
Control vs. x-Rs	-2.587	<b>0.010</b>	-3.086	<b>0.002</b>	-0.237	0.813
Control vs. x-Ea	-1.551	0.121	-2.848	<b>0.004</b>	-0.277	0.782
Control vs. x-Rt	-0.268	0.962	-4.731	< <b>0.001</b>	-2.989	<b>0.004</b>
Control vs. x-Bb	-1.905	0.057	-2.154	0.031	-0.148	0.882

Control|=water, x Rs=R. *sirenisis* extract, x Ea=E. *anthonyi* extract, x Rt=R. *temporaria* extract, x Bb=B. *bufo* extract

observed between the control and the groups exposed to conspecific extracts of x-Bb and heterospecific extracts of x-Rs and x-Ea.

## Discussion

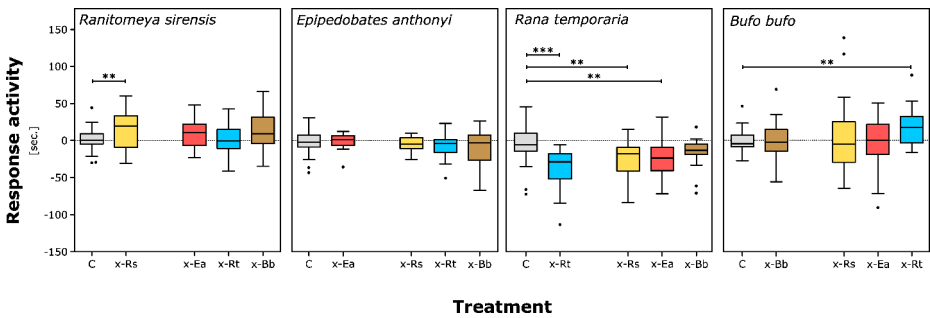
In this study we focused on the perception and responses to injury cues (alarm cues) in dendrobatid tadpoles, specifically emphasizing *Ranitomeya sirensis* and *Epipedobates anthonyi*. Additionally, we broaden our study to include tadpoles and injury cues from *Rana temporaria* and *Bufo bufo*, enabling us to explore the perception of heterospecific responses among all the aforementioned species, each with distinct ecological niches and degrees of sociality. We hypothesized diverse responses to con- and heterospecific injury cues among tadpoles, with variations attributable to differences in their degree of sociality, habitat constraints and phylogenetic relationships.

Our results diverge from the predictions made in hypotheses (Hy1), (Hy2), and (Hy3b). Contrary to expectations, *R. sirensis* tadpoles increased their activity when exposed to conspecific injury cues. Furthermore, *E. anthonyi* and *B. bufo* tadpoles did not show reduced activity levels as anticipated in response to con- and heterospecific cues (with the exception of increased activity of *B. bufo* tadpoles towards *R. temporaria* cues). Our findings do, however, support hypothesis (Hy3a), as *R. temporaria* tadpoles exhibited reduced activity in response to both con- and heterospecific cues, with varying levels of intensity.

### Tadpole response - *Ranitomeya sirensis*

Contrary to our prediction (Hy1), *R. sirensis* tadpoles increased not decreased their activity towards conspecific injury cues. The increased activity towards conspecific injury cues may suggest a chemically mediated agitation or cannibalistic behavioural response (potentially related to feeding behaviour; Spieler and Linsenmair 1999; Hagman 2008), considering the species' solitary lifestyle and latent aggressive behaviour towards conspecific competitors (personal observation). Previous studies have reported facultative, opportunistic cannibalism in several genera of poison dart frogs (Caldwell and De Araújo 1998; Gray et al. 2009; Rojas 2014; Dugas et al. 2016), including *Ranitomeya* (Summers 1999; Summers and Symula 2001; Poelman and Dicke 2007; Schulte et al. 2011; Brown et al. 2011; Schulte 2014). Meaning that due to the risk of reducing inclusive fitness by consuming close relatives, many tadpoles consume only conspecifics that are already deceased or weakened. The evolution of such behaviour in dendrobatids is likely driven by increased parental investments and limited resources for tadpoles in their environment (Caldwell and De Araújo 1998; Summers 1999; Summers and McKeon 2004; Carvajal-Castro et al. 2021). Since injury cues are involuntary released substances during predation events (Hettzey et al. 2015; Wisenden 2015) and likely associated with potential nutrient-rich carcasses, the perception of these stimuli likely triggers an altered perception of increased nutrient availability in facultative cannibalistic tadpoles. This, in turn, induces feeding behaviour, which is associated with increased levels of activity.

Surprisingly, however, *R. sirensis* tadpoles did not respond to heterospecific injury cues, raising the question of the adaptive advantage of this discriminatory behaviour towards injury cues. If aggressive behaviour enhances survivorship and reproductive output, aggres-



**Fig. 1** Short term changes in activity (response activity) in tadpoles of *Ranitomeya sirens*, *Epipedobates anthonyi*, *Rana temporaria* and *Bufo bufo* after experiencing extracts of: *R. sirens* (x-Rs), *E. anthonyi* (x-Ea), *R. temporaria* (x-Rt), *B. bufo* (x-Bb) or water (i.e. control) during behavioural trials. Trials with extracts from conspecific tadpoles are arranged next to the control (C) on the left side, trials with heterospecific extracts on the right side of each panel. \*\*\*\* $P < 0.001$ , \*\* $< P < 0.01$ , in post hoc Mann-Whitney U pairwise comparisons of treatments vs. control (alpha value adjusted for four comparisons per species;  $P = 0.0125$ )

sive cannibalism, as seems to be the case in *R. sirens*, may be favoured by natural selection (Bobisud 1976; Jones 1982; Stenseth 1985). This is because traits accelerating tadpole development or increasing body size at metamorphosis can confer advantages such as earlier reproductive maturity or larger body size at maturity (Wilbur 1980; Werner 1986; Smith 1987), rendering in-discriminatory elimination of competitors (Crump 1992) and potential predators (Caldwell and De Araújo 1998) a beneficial fitness increasing trait (Bobisud 1976; Jones 1982; Stenseth 1985). As many poison dart frog species deploy their offspring individually and often actively avoid phytotelmata with conspecific competitors (Brust 1993; Caldwell and De Araújo 1998; Summers 1999; Poelman and Dicke 2007), the potential cost of reducing their inclusive fitness, should become minimal, thus facilitating the evolution of in-discriminatory aggression or cannibalism even more. Our results, however, suggest a specialised recognition system that targets conspecific competitors and might be the results of an isolated evolutionary history mediated by selective individual tadpole deposition in unoccupied phytotelmata (Brust 1993; Caldwell and De Araújo 1998; Summers 1999; Poelman and Dicke 2007; Schulte et al. 2011) that left tadpoles of *R. sirens* unable to perceive or interpret heterospecific cues appropriately (but see Schulte and Lötters 2014). Although evidence suggests that conspecific cannibalism may provide greater benefits compared to consuming heterospecifics due to proper proportion of nutrients (Nagai et al. 1971; Meffe and Crump 1987; Crump 1990; Wildy et al. 1998), future studies should delve deeper into the factors influencing these responses (e.g. naturally occurring heterospecific interactions among dendrobatids).

### Tadpole response - *Epipedobates anthonyi*

Contrary to our hypothesis (Hy2), *E. anthonyi* tadpoles did not exhibit any observable behavioural response to the tested injury cues (i.e. neither con- nor heterospecific). Our results suggest that chemical cues associated with acute predation events do not mediate anti-predator responses in this species. A potential reason would be associated with the information transmission characteristics. While chemical cues possess advantageous long-

lasting properties that facilitate the perception and fine-tuning of anti-predator mechanisms, their information transmission may be insufficient (i.e. too slow and non-directional) compared to other modalities such as acoustic and visual cues (Bradbury and Vehrencamp 2011). This limitation could reduce chemical communication's utility and adaptive benefits in anti-predator contexts in small water bodies, especially in situations with rapidly escalating predator-prey interactions. In contrast, the rapid transmission of information within a short timeframe becomes crucial in spatially limited environments, such as puddles or low-current bays in rivers. However, evidence suggests that tadpoles have poor vision (Manteuffel et al. 1977; Hoff et al. 1999; Eluvathingal et al. 2009), which can be further impaired in murky, turbulent, or densely vegetated water bodies where tadpoles are commonly found (McDiarmid and Altig 1999; Wells 2007). Indeed, *E. anthonyi* tadpoles appeared unaffected by approaching shrimp nets, shadows, or movements just above the water level until close proximity (personal observation).

In spatially limited aquatic environments, like puddles or low-current bays in tropical rainforests, alternative modalities such as short-range communication may play a more significant role. Unlike chemical cues, stimuli like touch and hydrodynamic cues can rapidly convey information and are highly effective over short distances, particularly when vision is impaired (Bradbury and Vehrencamp 2011). Similar to chemical cues, these cues possess advantageous properties and are vital for many aquatic predators and prey organisms (Bradbury and Vehrencamp 2011). Generating hydrodynamic cues, including currents, vortices, and surface disturbances, is inherent to locomotion in predominantly aquatic organisms (i.e. involuntary generated) and can provide valuable information to prey animals about the size, speed, and shape of the generating organism (Hanke et al. 2000; Coombs 2001). In fact, numerous aquatic organisms rely on hydrodynamic cues to track prey (Bleckmann 1994; Dehnhardt et al. 1998, 2001; Pohlmann et al. 2001, 2004; Schulte-Pelkum et al. 2007) or detect nearby predators and navigate their environments through hydrodynamic communication (Hassan 1986; Budelmann and Bleckmann 1988; Gray and Denton 1991; Budelmann 1995; Coombs and Montgomery 1999; Mogdans et al. 2002; Burt De Perera 2004; Janssen and Strickler 2006; Platvoet et al. 2007; Bradbury and Vehrencamp 2011).

Given that tadpoles have well-developed lateral line systems (Lannoo 1987; McDiarmid and Altig 1999), and considering dendrobatid interactions in which visual and tactile cues are of more importance (e.g. mother offspring communication; Stynoski and Noble 2012), the potential involvement of short-range modalities in anti-predator mechanisms of *E. anthonyi* tadpoles remains plausible. Moreover, blind cave fish actively generate turbulences while moving and rely on distortions in reflected eddies and vortices to detect and warn conspecifics about obstacles in their proximity (Hassan 1986; Burt De Perera 2004), leaving room for speculation about sophisticated use and interpretation of hydrodynamic cues in *E. anthonyi* tadpoles. Likewise, there is the possibility that responses to avoid predation may have remained undetected within the confines of our experimental design (e.g. limited space with no options for tadpoles to escape or hide and undetected behavioural changes immediately after the introduction of cues in the stimulus phase). Anti-predator behaviour is often more intricate and may also manifest in spatial avoidance and increased hiding behaviour (Teplitsky and Laurila 2007; Eterovick et al. 2010; Szabo et al. 2021).

Both assumptions regarding the utilization of short-range modalities and more intricate behavioural changes are supported by observations during husbandry activities. In these instances, *E. anthonyi* individuals displayed heightened sensitivity to water body move-

ments and surface disturbances. Tadpoles exhibited rapid, agile swimming responses when encountering unusual water movements or disturbances in close proximity, often resulting in shelter-seeking behaviour. Therefore, our results lead us to postulate that tadpoles of *E. anthonyi* employ distinct short-range modalities and behavioural responses to avoid predation, which may extend beyond activity adjustments and include behaviours such as rapid shelter-seeking. Consequently, further investigations are necessary to explore alternative sensory modalities and anti-predator strategies employed by *E. anthonyi* tadpoles in their natural environment.

### Tadpole responses - *Rana temporaria* & *Bufo bufo*

Contrary to our expectations outlined in hypotheses (Hy3a) and (Hy3b), our study reveals notable inter-species differences between *R. temporaria* and *B. bufo*. Specifically, our results provide support only for hypothesis (H3a). Tadpoles of *R. temporaria* exhibited a reduced activity response to conspecific injury cues, consistent with previous research (Laurila 2000; Laurila et al. 2004; Marquis et al. 2004; Mandrillon and Saglio 2009; Hettyey et al. 2015), while demonstrating a milder reaction to heterospecific cues. In contrast (Hy3b), *B. bufo* tadpoles did not exhibit the expected reduction in activity in the presence of either conspecific or heterospecific cues, deviating from prior research findings with conspecific injury cues (Marquis et al. 2004; but see Rödin-Mörch et al. 2011). Instead, *B. bufo* tadpoles displayed an increase in activity when exposed to cues from *R. temporaria*.

Literature suggests that the phylogenetic relationship and shared evolutionary history among species contribute to heterospecific responses due to the presence of similar metabolites and specialised mixture compositions (Mirza and Chivers 2001; Dalesman et al. 2007; Ferrari et al. 2007, 2008a, 2009a; Ferland-Raymond and Murray 2008; Mitchell et al. 2012, 2017). Therefore, the diminished response of *R. temporaria* to heterospecific cues may be attributed to the phylogenetic distance between the species involved and the presence of phylogenetically conserved or convergent elements of injury cues mediating anti-predator behavioural responses (Ferrari et al. 2010). However, the evolution of injury cues remains largely unclear but may be facilitated through kin-selection (Ferrari et al. 2010; Chivers et al. 2012; see also Wisenden 2015 for a comprehensive list of hypothesis).

The responses of bufonid tadpoles to heterospecific injury cues have been shown to be quite variable in previous studies, ranging from “no response” (Hagman and Shine 2009), decreased activity (Summey and Mathis 1998; Hagman and Shine 2009), attraction/foraging (Petranka 1989; Hagman and Shine 2009), to avoidance behaviour (Hews and Blaustein 1985). In our experimental setup using cups, behavioural responses such as attraction/foraging and avoidance would translate into increased activity levels. This is because, increased movement may be utilized by feeding tadpoles to churn up food particles from the pond floor (Spieler and Linsenmair 1999; Hagman 2008), or as an attempt to escape the area (i.e. the cup) associated with elevated predation risk (Rödin-Mörch et al. 2011). Consequently, it remains uncertain whether the response exhibited by *B. bufo* tadpoles to injury cues from *R. temporaria* represents attraction to a food source or an escape strategy.

Between-species differences in the context of anti-predator behaviour between *R. temporaria* and *B. bufo* have previously been reported by Laurila et al. (1997). Although they investigated behavioural responses to different types of cues (i.e. predator-borne cues), their findings align with those of our study (i.e. no activity reduction in *B. bufo* tadpoles

but observed reductions in *R. temporaria* tadpoles), and suggest that such differences may result from variations in species-specific predation risks as well as costs associated with anti-predator behaviour (e.g. energetic and opportunity costs; Lima and Dill 1990; Laurila et al. 1997; Lima and Bednekoff 1999; Ferrari et al. 2009b). Studies have shown that anti-predator behaviour, such as decreased activity, can lead to reduced growth rates and smaller size at metamorphosis (Holomuzki 1986; Skelly and Werner 1990; Skelly 1992), ultimately impacting lifelong reproductive success (Smith 1987; Semlitsch et al. 1988; Berven 1990; Scott 1994). Given that *R. temporaria* and *B. bufo* tadpoles can coexist in dense populations (Laurila et al. 1997; Bardsley and Beebee 1998; Nyström and Åbjörnsson 2000; personal observation of our study system), the expression of behavioural anti-predator behaviour might lower their competitive abilities. Therefore, maintaining high activity levels in *B. bufo* (Chovanec 1992), may be favoured to prevent a loss of competitive ability (Laurila et al. 1997). Furthermore, *B. bufo* possesses inherent physiological defence mechanisms (i.e. noxious skin compounds; Flier et al. 1980) that render it unpalatable to certain predators (Griffiths and Denton 1992; Semlitsch and Gavasso 1992). In contrast, *R. temporaria* lacks such additional defence mechanisms and therefore might face a generally higher risk of consumption by predators compared to *B. bufo* (Álvarez and Nicieza 2009). This disparate predation risk could explain why *B. bufo* maintains its activity levels while *R. temporaria* exhibits anti-predator behaviour (Laurila et al. 1997).

### Study limitations

Given tadpoles in this study were all predator naïve, our results point towards innate response and thus do not account for potential undetected behavioural responses mediated by learning (i.e. past experiences with additional predator-borne cues; Suboski 1990; Mirza and Chivers 2000; Dalesman et al. 2006; Mirza et al. 2006; Ferrari et al. 2010). Moreover, although prey-borne injury cues can elicit behavioural responses in isolation (e.g. Marquis et al. 2004; Fraker et al. 2009; Rödin-Mörch et al. 2011; Hettzey et al. 2015), evidence suggests that additional presence of predator kairomones may be necessary for a complete manifestation of short term induced defences (Petranka and Hayes 1998; van Buskirk and Arioli 2002; Schoeppner and Relyea 2005, 2009; Richardson 2006; Hettzey et al. 2010, 2015; Hemnani et al. 2022). Future research should therefore also strongly consider including predator odours and diet cues (Mitchell et al. 2017), to be able to formulate more reliable conclusions about chemically induced short term anti-predator mechanisms in poison dart frog tadpoles (e.g. Szabo et al. 2021).

Lastly, our study is limited to conclusions about individual tadpole responses. In fish, predator avoidance behaviour triggered by injury cues can be influenced by group size (Surova et al. 2009) and disturbance cues can lead to tighter group cohesion and increased coordination (Bairos-Novak et al. 2019; Crane et al. 2020). Given that tadpoles also exhibit group formation based on familiarity or kinship (Waldman and Adler 1979; Halverson et al. 2006; Eluvathingal et al. 2009; Pizzatto et al. 2016), tadpoles of socially oriented species involved in our study (i.e. *E. anthonyi*, *R. temporaria*, and *B. bufo*) may demonstrate different group-level responses compared to individual responses. Future research should therefore incorporate more complex bioassays (e.g. testing groups of tadpoles) and deploy more complex quantitative measures to elucidate the full range of anti-predator responses in these species. Particularly exploring the degree of sociality of *E. anthonyi* and the extent of their

gregarious behaviour would provide valuable insights into their microhabitat preferences and potential kin associations mechanisms (e.g. attraction to conspecifics vs. repulsion from heterospecifics; Eluvathingal et al. 2009).

## Conclusion

Our study provides preliminary insights into the chemical alarm cue response system of Neotropical poison dart frog tadpoles in comparison to species inhabiting temperate climates. In contrast to species such as ranids and bufonids, which exhibit social behaviour and inhabit large permanent pools characterised by intricate ecological communities and significant predator pressure, dendrobatid tadpoles, residing solitarily or in small sibling groups within small or ephemeral pools, solely responded to conspecific cues or displayed no response to chemical cues altogether. Being the first investigation of perception and responses to con- and heterospecific injury cues (alarm cues) in dendrobatid tadpoles, this research prompts new questions and ideas regarding the ecological significance and evolution of chemical communication in species facing limited resources and reduced predator pressure during development. Further investigations are needed to explore the factors influencing these responses, investigate alternative sensory modalities, and elucidate the anti-predator strategies employed by different tadpole species in their natural environments. Moreover, our study underscores the necessity of comparative research for a comprehensive understanding of chemical communication in different aquatic ecosystems and developing new ideas for the evolution of chemical alarm systems and the substances involved in conveying information's about environmental risks.

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**Authors' contributions** KL & LMS developed the study idea. KL collected tadpole egg masses. DAA established the poison frog breeding colonies & KL the tadpole husbandry. KL and DAA established the research protocol and conducted experiments. KL extracted and analysed the data. KL and LMS conceptualised the framework and outline of this manuscript. KL took the lead in writing the manuscript. All authors provided critical feedback, helped finalising the manuscript, and gave final approval for publication.

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**Data Availability** Upon acceptance the data underlying this article is available on request from the corresponding author.

## Declarations

**Competing interests** The authors declare no competing interests.

**Consent for publication** All co-authors have approved the manuscript for publication.

**Ethics approval** All animal handling and research in this study followed the guidelines of the country where they were performed (Germany, Hesse) and were approved by the “Regierungspräsidium Darmstadt” (references: V54-19c20/211-FR Biologicum & V54-19c18-FR/1022) and the “Hessisches Landesamt für Naturschutz, Umwelt und Geologie” (reference: N2-103s0601/2020-3-06).

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