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ORIGINAL ARTICLE

Mother-offspring chemical communication and tadpole aggregation in a neotropical foam-nesting frog

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Abstract

Communication during parental care is important in the context of offspring defence and parent-offspring recognition. In aquatic environments, chemical communication is usually the most effective and plays different roles in parental behaviour in many groups of animals. Attending females of some Neotropical anurans (*Leptodactylus*) lead entire schools of tadpoles through the water. However, little is known about how attending females communicate with the tadpoles or whether this communication is mother-offspring specific. We therefore conducted behavioural experiments with *Leptodactylus podicipinus* to address these questions. Initially, we investigated how visual, tactile, and chemical stimuli from attending females affect the aggregation behaviour of tadpoles. Next, we compared the effects of the chemical stimulus from attending females with those from other conspecifics (non-attending females and males) on schooling behaviour. Finally, we tested whether tadpoles preferred to be aggregated next to familiar attending females instead of unfamiliar ones. Our results indicated that only the chemical stimulus from attending females, and not visual or tactile, increased the time that tadpoles remained aggregated. The chemical stimuli from non-attending females and males did not affect tadpoles' behaviour. However, contrary to our expectations, we did not find a school preference for familiar attending females. Our study is the first showing that chemical stimulus is important for mother-tadpole communication in a *Leptodactylus* species, playing a crucial role in tadpole aggregation and attraction. Future studies including other species should address the nature of the chemical compounds and their role, if any, in kin recognition in these frogs with aquatic maternal care.

Significance statement

Parent-offspring communication is not well understood in anurans. Females of some frog species in the genus *Leptodactylus* protect and guide schools of tadpoles in aquatic habitats and tactile, chemical and visual communication may be involved. Through our experiments, we found that only chemical stimulus from attending females had a positive effect on tadpoles´ aggregation time and attraction, playing an important role in school cohesion. Additionally, there were no differences in tadpoles´ responses to chemical stimuli from familiar and unfamiliar females, which may increase tadpoles´ survival chances. In these cases, however, the costs and benefits for attending females and tadpoles are yet to be addressed. Although tactile and visual stimuli deserve more investigation, we showed that parent-offspring chemical communication in this frog species is effective, leading to school cohesion, consequently favouring protection of tadpoles by their mothers.

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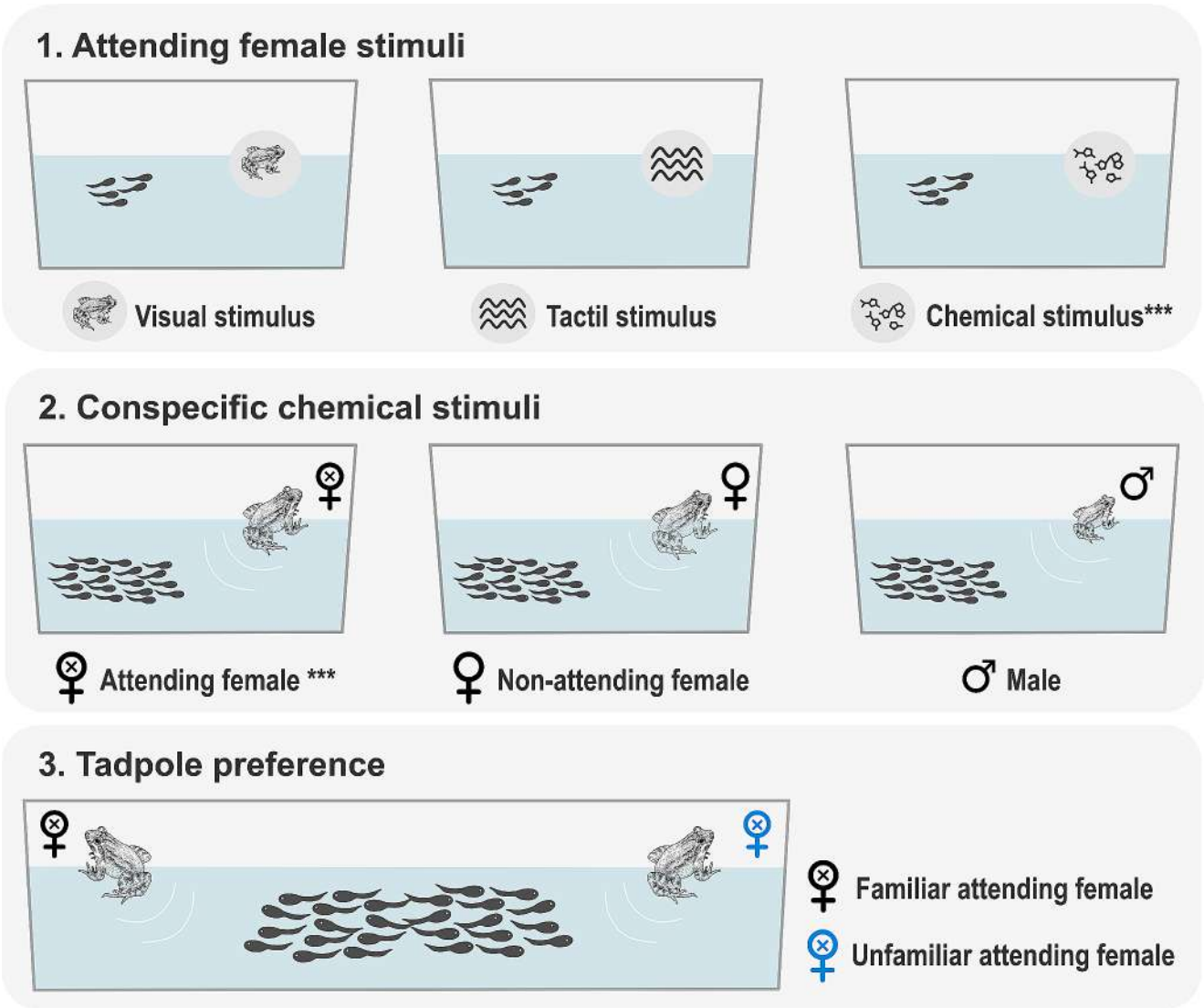
Graphical Abstract



Keywords *Leptodactylus* · Parent-offspring interaction · Tadpole schooling · Kin recognition · Maternal care

Introduction

Communication is defined as the transmission of information from a sender to a receiver, resulting in a change in the receiver's behaviour (Kaplan 2014). Animal communication can be intraspecific or interspecific, and plays many important functions, including territorial defence, rival warning, courtship behaviour, prey location, parent-offspring interaction and kin recognition to avoid alloparental care (Jacot et al. 2010; Bradbury and Vehrencamp 2011; Wyatt 2014; Coombes et al. 2018). The information flows through diverse stimuli such as signals or cues with multiple purposes (Brunetti et al. 2018). Signals are those that are emitted voluntarily to produce an expected effect on the receiver, usually leading to changes in behaviour (Bro-Jørgensen 2010; Schulte et al. 2015; Brunetti et al. 2018). Cues, on the other hand, are those stimuli that are produced involuntarily by the sender, but with relevant information to the receiver (Schulte et al. 2015).

Different types of signals are used in animal communication, such as visual, acoustic, chemical, tactile or magnetic (Mattey et al. 2018). Chemical signals are the most ancient and widespread form of animal communication, commonly used during courtship (Johansson and Jones 2007; Meinwald and Eisner 2008; Wyatt 2014). However, they also play a fundamental role in parental care, such as during

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offspring begging behaviour in insects and anurans (Kam and Hang 2002; Smiseth et al. 2010), during feeding behaviour in birds and mammals (Schaal et al. 2003; Balthazart and Taziaux 2009), and for mutual parent-offspring recognition in beetles and mammals (Schaal et al. 2003; Smiseth et al. 2010). In aquatic environments, chemical signalling has several advantages, as the transmission of acoustic and visual signals can be hindered and less effective (Brönmark and Hansson 2000; Rosenthal and Ryan 2000). Chemical communication in aquatic environments, for instance, can be used by parents to guide and maintain cohesion of offspring, as observed in non-gregarious cichlids and suggested for anurans with schooling behaviour (Myrberg 1975; Barnett 1977; Wells and Bard 1988).

Aggregation is a common social behaviour of aquatic organisms, in which they come together and perform coordinated movements with adaptive functions (Pavlov and Kasumyan 2000). This behaviour is well known in fish and tadpoles, proving to be an effective anti-predator strategy by diluting the risk of predation within the group and confusing predators (Hobson 1978; Caldwell 1989; Lehtonen and Jaatinen 2016). Tadpoles from 12 anuran families are known to exhibit aggregation behaviour (Wells 2007). In Neotropical leptodactylid frogs, tadpole aggregation behaviour depends on external social stimuli (Ponssa 2001) and is usually accompanied by parental care (e.g. Wells and Bard 1988; Martins 2001). For instance, within species of the *Leptodactylus melanonotus* and *L. latrans* groups, females attend to eggs and guide aquatic tadpole schools, dig channels to connect water bodies, and protect offspring from predators by displaying aggressive behaviours (Wells and Bard 1988; Prado et al. 2000; Martins 2001; Rodrigues et al. 2011; Castro et al. 2013; Sestito et al. 2016; Carrillo et al. 2023).

In these *Leptodactylus* species with maternal care, females perform a "pumping" behaviour (sensu Wells and Bard 1988) that may aid in tadpole orientation and guidance. In this behaviour, the attending female hits the water surface with her pelvis to generate waves and tadpoles follow and scrape the female´s back and legs (Wells and Bard 1988; Martins 2001; Wells 2007; Castro et al. 2013; Carrillo et al. 2022; Fig. 1). Besides the tactile stimulation caused by the pumping behaviour, chemical signalling has been pointed out as important to attract, orient, aggregate, and guide tadpoles through obstacles to deeper aquatic sites (Wells and Bard 1988; Vaira 1997; Hoffmann 2006). Thus,

Fig. 1 Attending female of *Leptodactylus podicipinus* with its school of tadpoles at Poconé, Mato Grosso state, Brazil. Notice the tadpoles scraping the female´s back and legs. Photo by Harry W. Greene

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the communication between attending females and schools of tadpoles may involve, at least, three different stimuli: visual, tactile, and chemical. However, this prediction has never been tested experimentally, and parent-offspring communication in anurans remains poorly understood.

Taking all of this into consideration, we aimed to investigate mother-offspring communication in a Neotropical foam nesting frog, *Leptodactylus podicipinus*. Based on previous studies and field observations, we conducted three independent experiments to test the following hypotheses: (1) Given the importance of chemical communication in aquatic habitats, we hypothesize that chemical stimulus is the most effective in promoting aggregation of tadpoles. Thus, we predict that tadpoles will spend more time aggregated under a chemical stimulus from an attending female than under visual or tactile stimuli. (2) If chemical communication is important for mother-offspring interaction, we hypothesize that only attending females should produce a chemical signal/cue to promote tadpole aggregation compared to conspecific adults (non-attending females and males). Therefore, we predict that tadpoles will spend more time close to the attending female than close to conspecifics. (3) Finally, if there is a positive correlation between offspring relatedness and parental care frequency, we hypothesize that tadpoles should be able to discriminate chemical stimulus of familiar attending females from those emitted by unfamiliar attending females. Our prediction is that tadpoles will prefer to aggregate next to familiar attending females rather than unfamiliar ones, due to the presumed genetic relationship.

Methods

During the rainy seasons of 2019 and 2021 (November to March), we collected attending females of *Leptodactylus podicipinus* with their tadpole schools at the Estância Criola ranch (20°32'13.51"S, 55°32'53.69"W). Estância Criola is located in a Cerrado area in the state of Mato Grosso do Sul, central Brazil, considered the most diverse tropical savannah and one of the most important hotspots for global conservation due to its high biodiversity and pressing threats (Eiten 1994; Myers et al. 2000; Alvares et al. 2013).

In the Cerrado, the reproductive activity of *Leptodactylus podicipinus* (Fig. 1) is restricted to the rainy season from November to January (JFC Carrillo pers. obs.) and females attend large schools until the end of the metamorphosis (Martins 2001). We captured a total of 14 schools of *L. podicipinus* with their attending females. *Leptodactylus podicipinus* schools had an average of 404 and standard deviation (±) of 173 tadpoles (range = 112–701; $N = 14$). The schools presented tadpoles of different stages of development (Gosner 1960): seven schools had tadpoles of one stage of development, four schools had tadpoles of two different stages of development, and three schools had tadpoles of three different stages of development (Supplementary 1). We captured the animals and maintained adults in separated aquariums (40 × 20 × 30 cm), containing vegetation and water from the collection site, and tadpoles in aquariums with water and oxygen pumps. Individuals remained in captivity for a maximum of two days. After the experiments, all adults and tadpoles were anesthetized and euthanized following the Brazilian bioethics legislation (CEUA/UFMS #1.085/2019), preserved in 90% alcohol for future genetic analyses, and stored at the zoological collection of the Universidade Federal de Mato Grosso do Sul (ZUFMS-AMP – 14,661–14,668, 14,670–14,698, 14,710–14,723).

Experiment 1 was designed to investigate which type of stimulus (visual, tactile, or chemical) used by attending females was more effective in promoting tadpole aggregation, on a small scale, using only five tadpoles per replicate. Once we identified the effects of chemical stimulus on tadpole aggregation (see Results), the experiment 2 tested whether tadpoles responded only to the chemical stimulus produced by attending females, or by other conspecifics as well, by using the entire schools and the adults (attending female, non-attending female, male) as stimulus source. Additionally, we made behavioural observations to describe school behaviour. The experiment 3 intended to address whether tadpoles prefer to aggregate next to familiar attending females over unfamiliar attending females. To minimize observer bias, blinded methods were used when all behavioural data were recorded and/or analyzed.

Experiment 1: attending female stimuli

After capture, we transported all individuals to the Laboratory of Ecology of the Universidade Federal de Mato Grosso do Sul (UFMS, Campo Grande, MS, Brazil). Animals were transported in coolers with compartments containing water from the sample site, separating schools from attending females. Later, we placed each school in separate aquariums without the attending female for one day of acclimation at ambient temperature (27–29 °C) and a 12 to 12 h photoperiod.

The following day, we conducted three trials of each treatment (visual, tactile, or chemical stimulus) and their respective controls, with 12 replicates per trial. To test for tadpole aggregation in response to the visual stimulus, we used a plastic frog doll with the same coloration pattern of *L. podicipinus* adults to simulate attending female presence (visual stimulus) and a plastic ball as a control. To test for tadpole aggregation in response to tactile stimulus (attending female pumping behaviour generating waves), we simulated the rhythmic pattern of pumping with a

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hanging cylinder (5 mm radium and 60 mm long) by tapping the water multiple times while increasing the rhythm as described by Martins (2001). We used the same cylinder, this time without movement, as a control. To test for tadpole aggregation in response to chemical stimulus, we extracted the attending female´s skin secretion with a cotton ball using a mild electric stimulation (see Tyler et al. 1992) and we used a fresh sterile cotton ball as a control. For each experiment, we placed five *L. podicipinus* tadpoles from the same school in Petri dishes (150 mm of diameter) filled with fresh rainwater (changing it for each trail), guaranteeing enough vertical water space for swimming (15 mm). After three minutes of acclimatization in the Petri dish, we placed the corresponding stimulus fixed to the border. For each replica, we used different tadpoles. For further details of the experiments see Supplementary 2.

Tadpoles' behaviour was recorded on video for seven minutes. Aggregation time (cumulative time of tadpoles aggregating) was registered using the Behavioural Observation Research Interactive Software BORIS (Friard and Gamba 2016). Two tadpoles together may be fortuitous and three or more staying together can be considered intentional. Therefore, for the purpose of this experiment, we defined aggregation time as the time that three or more tadpoles remained in contact or moved together in the same direction (see Pavlov and Kasumyan 2000). For each trial (visual, tactile, and chemical signal experiments), we fitted a linear mixed effect model in R 4.0.4. (R Core Team 2021), with aggregation time as the response variable, treatment (stimulus vs. control) as fixed factor and school as random intercept, using the *nlme* package (Pinheiro et al. 2021).

Experiment 2: intraspecific chemical stimuli

For this experiment, we used seven complete schools and their respective attending females, different individuals from those used in experiment 1. For the purpose of this experiment, in addition to attending females and tadpoles, we also collected males and non-attending females (females that were not caring for tadpoles). After field collection, the entire school of *Leptodactylus podicipinus* was placed in a tank (350 × 240 mm) filled with pond water collected at the sample site. The stimulus was placed in one of four quadrant corners. For every trial replicate (seven controls, seven males, five non-attending females and six attending females), we changed the stimulus corner position randomly and waited at least 10 min between replicates to allow water homogenization. The stimulus consisted of an opaque cup with holes containing one of three adult conspecifics: attending female, non-attending female or male. As a control we used an opaque cup without holes with an attending female (Supplementary 3). The behaviour of each tadpole was video recorded for seven minutes. We made behavioural observations to describe schooling features and we registered aggregation time (seconds) using BORIS software (Friard and Gamba 2016). This time we defined aggregation time as the time that more than 90% of the tadpoles maintained contact or moved together in the same direction (see Pavlov and Kasumyan 2000). To test if the attending females were able to attract tadpoles, aggregation time was divided into two variables, aggregation time close to the stimulus and aggregation time far from the stimulus. Aggregation time close to the stimulus was the time tadpoles were grouped in the quadrant corner where the cup with the adult was placed (Supplementary 3). Aggregation time far from the stimulus was the time tadpoles were grouped in any quadrant corners where the cup with the adult was not placed. As the data from this experiment did not meet the criteria for parametric statistics, it was analysed by Kruskal-Wallis and post-hoc Dunn tests in R 4.0.4 (R Core Team 2021).

Experiment 3: school preference for familiar or unfamiliar attending female

Experiment 3 follows the guidelines and analyses employed in experiment 2. Using three schools from experiment 2 and their respective attending females, we measured tadpoles' aggregation time as follows. After placing the entire school in the middle of the tank, we simultaneously placed a familiar and an unfamiliar attending female in opposite corners of the tank (350 × 240 mm). We measured the aggregation time far from attending females, close to unfamiliar attending females, and close to familiar attending females (Supplementary 4). This procedure was repeated in six replicates with different tadpole schools. Besides the Kruskal-Wallis' test for cumulative aggregation time, we analysed how frequently tadpole schools aggregated next to familiar vs. unfamiliar attending females by a Chi-Square test in R 4.0.4 (R Core Team 2021).

Results

Experiment 1: attending female stimuli

Descriptive data of the three types of stimuli from attending females and controls tested are presented in Table 1. The aggregation time of *L. podicipinus* tadpoles differed significantly only in the chemical stimulus treatment, increasing from an aggregation time of 28.97 ± 19.13 s in the control to 113.98 ± 39.15 s in the chemical stimulus treatment ($t = 4.77$, $P < 0.001$, $N = 12$; Fig. 2). The aggregation time of the tadpoles did not vary significantly under visual and tactile stimulus when compared to their respective controls

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Table 1 Aggregation time (seconds) of the tadpoles of *Leptodactylus podicipinus* under three attending female stimuli (Experiment 1)

	Control				Stimuli			
	Mean	SD	Max	Min	Mean	SD	Max	Min
Chemical	28.97	19.13	59.35	2.57	113.98	39.15	154.23	40.11
Tactile	36.63	8.45	51.63	26.31	30.20	3.10	35.59	27.11
Visual	44.51	20.66	79.63	21.10	74.10	44.61	126.00	7.10

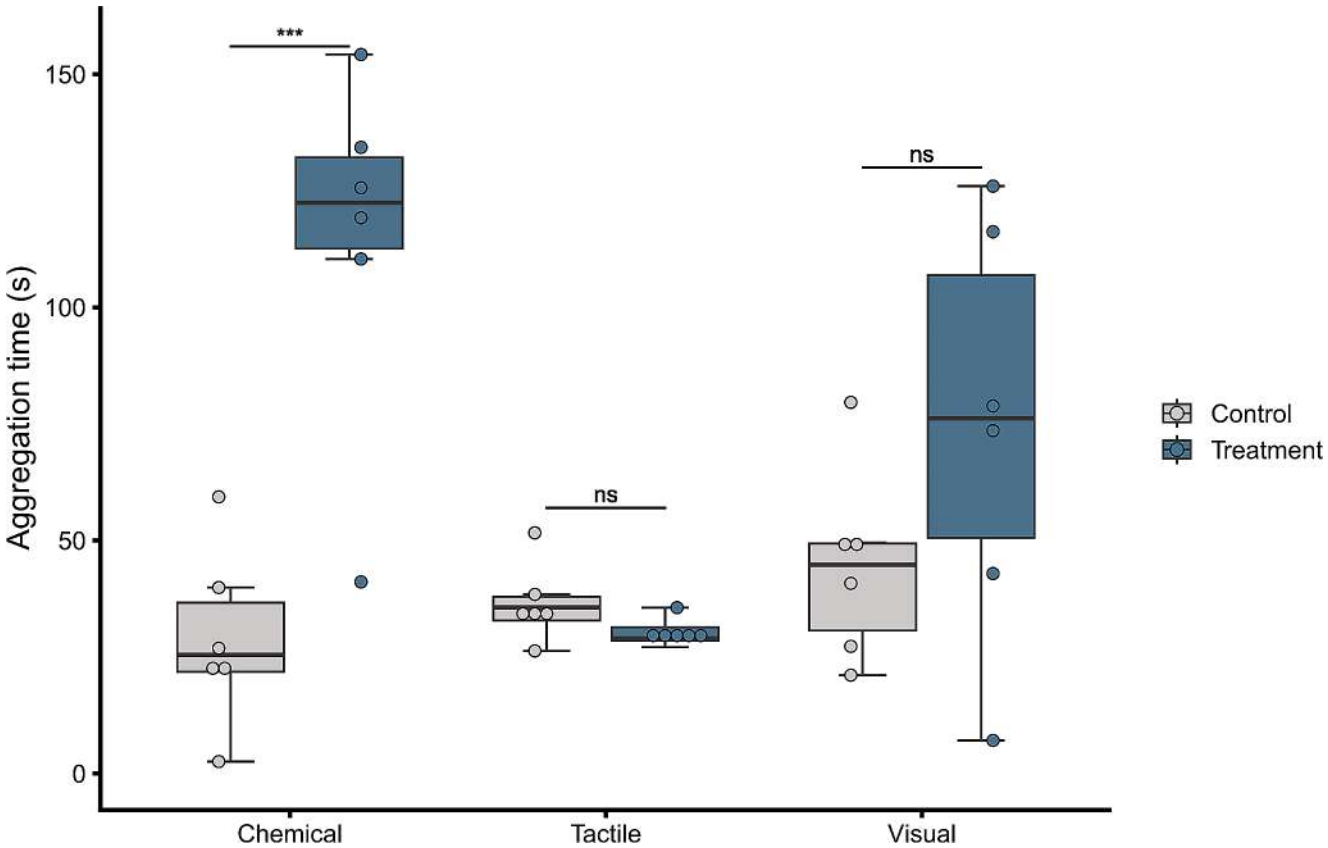

Fig. 2 Experiment 1. Boxplots of the cumulative aggregation time of *Leptodactylus podicipinus* tadpoles under three maternal stimuli (visual, tactile, and chemical) and their respective control trials. Boxes indicate the interquartile range (IQR), with the central line depicting the median and the whiskers extending to 1.5 * IQR. Points denote the individual data. $P < 0.001$ (***) and ns (non-significant)

($t = 1.47$, $P = 0.17$, $N = 12$; $t = -1.74$, $P = 0.11$, $N = 12$; respectively) (Fig. 2).

Experiment 2: intraspecific chemical stimuli

Tadpole schools of *L. podicipinus* presented two types of aggregation behaviour: constant movement aggregation and stationary aggregation (Supplementary 5). In constant movement aggregation, tadpoles moved all together in a cohesive way with limited space between them, following the edges of the tank. In stationary aggregation, tadpoles stayed at the bottom of the water, close to the stimulus, with space between them, and moved only to recover the lost position after water movement.

Measures of aggregation time and aggregation time next to the stimulus (male, non-attending female, attending female) for tadpole schools of *L. podicipinus* are presented in Table 2. We found differences in aggregation time close to the stimulus (Kruskal–Wallis test, $H = 16.65$, $P < 0.001$, $N = 25$). Specifically, the aggregation time of the control group was significantly different from that of attending females (Dunn = 3.12, $P < 0.001$), and similar to that of males and non-attending females (Dunn = 0.78, $P = 0.21$; Dunn = 0.23, $P < 0.40$; respectively) (Fig. 3). We did not find differences for the aggregation time far from the stimulus (Kruskal–Wallis test, $H = 6.27$, $P = 0.09$, $N = 25$).

Experiment 3: school preference for familiar or unfamiliar attending female

On average tadpoles spent more time aggregated next to the familiar attending female (230.01 ± 179.77 s) than next to

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Table 2 Aggregation time of tadpole schools of *Leptodactylus podicipinus* measured far from the stimulus (seconds) and aggregation time next to the stimulus (seconds) under three conspecific chemical stimuli: male, non-attending female, and attending female (Experiment 2)

	Aggregation close to the stimulus					Aggregation far from the stimulus				
	Mean	SD	Max	Min	*N*	Mean	SD	Max	Min	*N*
Control	3.94	7.29	18.63	0.00	7	29.09	28.62	74.71	0.24	7
Male	0.00	0.00	0.00	0.00	7	24.76	23.49	62.99	6.50	7
Non-Attending Female	1.20	2.68	6.00	0.00	5	10.12	11.05	28.84	0.00	5
Attending Female	244.84	108.94	366.00	107.88	6	89.9	86.55	222.11	0.00	6

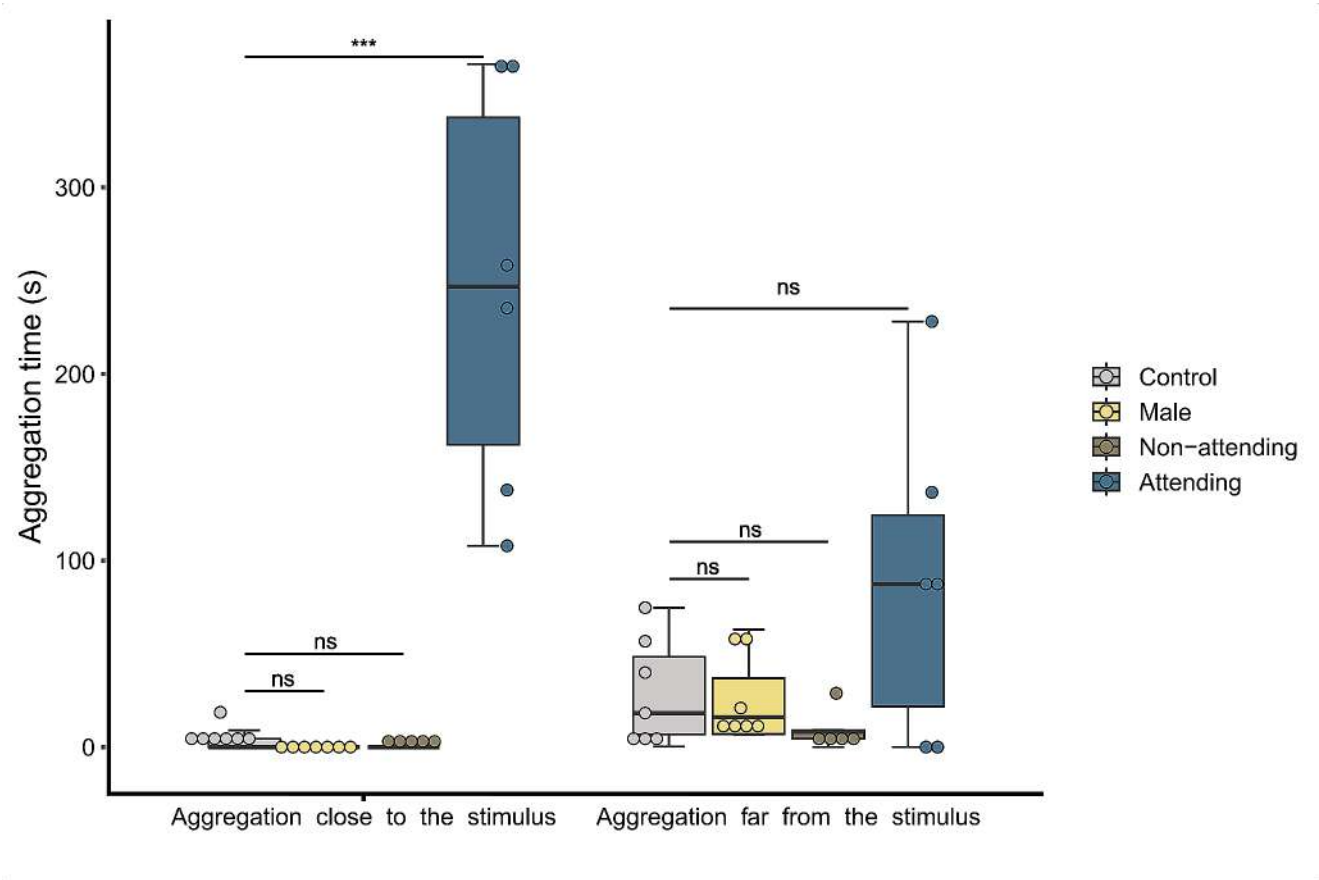

Fig. 3 Experiment 2. Boxplots of the school aggregation time of *L. podicipinus* under control (attending female in an opaque cup without holes) and chemical stimuli of conspecifics: males, non-attending females, and attending females. Boxes indicate the interquartile range (IQR), with the central line depicting the median and the whiskers extending to 1.5 * IQR. Points denote the individual data. $P < 0.001$ (***) and ns (non-significant)

the unfamiliar attending female (117.70 ± 182.35 s) or far from the female (14.64 ± 20.72 s). However, the time that tadpoles remained close to familiar or unfamiliar females did not differ significantly (Kruskal–Wallis test, H = 0.82, $P = 0.97$, $N = 6$; Fig. 4). Regarding school preference, we found no differences between tadpoles choosing to aggregate next to familiar or unfamiliar attending females (Chi-square test, $X^2 = 1.33$, $P = 0.24$, $N = 12$).

Discussion

We found that chemical stimulus produced by attending females plays an important role in mother-offspring communication in *Leptodactylus podicipinus* by increasing tadpole aggregation time, while visual or tactile stimuli had no effect when tested separately in our study. Pumping behaviour, in which attending females produce waves by hitting the water with their hips in rhythmic movements, is known in many species of *Leptodactylus* with maternal care of tadpoles (see Carrillo et al. 2023). In a previous study with *L. insularum* (referred as *L. bolivianus*), Wells

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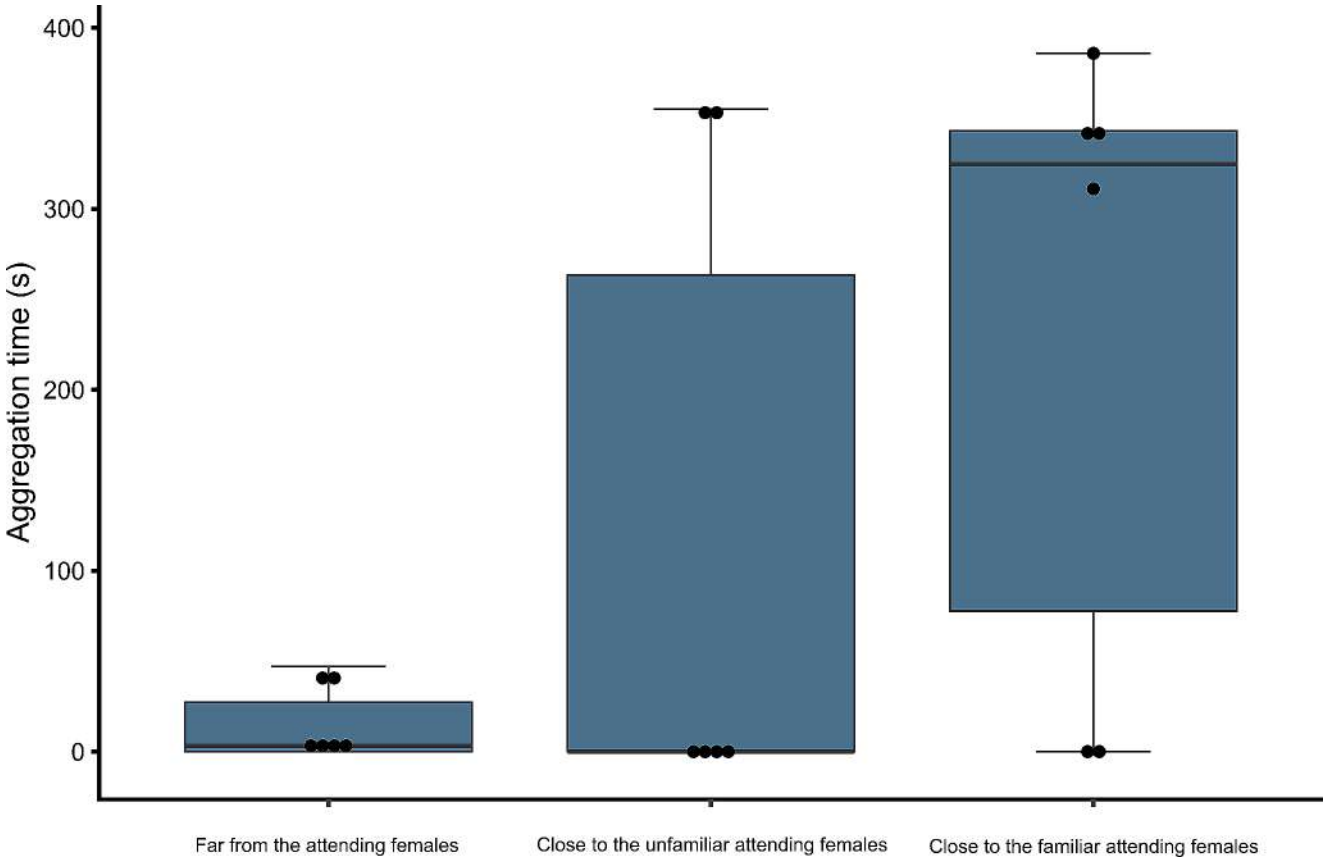

Fig. 4 Experiment 3. Boxplots of the school aggregation time far from the attending females, close to unfamiliar attending females and close to familiar attending females of *Leptodactylus podicipinus.* Boxes indicate the interquartile range (IQR), with the central line depicting the median and the whiskers extending to 1.5 * IQR. Points denote the individual data

and Bard (1988) pointed out that tadpole aggregation and attraction could involve not only tactile stimulus (waves) produced by the pumping of attending females, but also chemical communication. Accordingly, Hoffmann (2006) predicted a "beneficial or attractant" mucus secretion produced by the attending females to keep school cohesion and guidance. We did not find a tactile effect on schooling behaviour, likely because we isolated tactile from chemical stimuli. Because the pumping behaviour is common among attending females of *Leptodactylus* (e.g. Wells and Bard 1988; Martins 2001; Carrillo et al. 2022), we suggest that the main function of the waves produced by the pumping may be to spread the females´ chemical secretion through the water. Moreover, it is feasible that the different signals/cues emitted by attending females (e.g. visual, chemical, tactile) interact to produce school cohesion and tadpole attraction, which deserves further investigation.

In schooling animals, the main purpose of aggregation is to reduce the risk of predation (Manna et al. 2018). In fish, chemoreception plays a crucial role in aggregation and orientation, but only under particular circumstances (Hara 1975). At night (under low visibility), fishes aggregate using intraspecific chemical cues (Keenleyside 1955; Jones 1962), and at the daytime, in the presence of predators, they can aggregate by using alarm cues (Rüppel and Gosswein 1972). In anuran larvae, aggregation may depend on tadpole density, predator presence or warning cues (Ponssa 2001; Spieler and Linsenmair 2001). Although visual signals can contribute to school assembly, aggregation may also result from chemical communication among siblings (Blaustein and O'Hara 1982). Here we found a similar pattern for tadpole aggregation in a species with parental care, where the chemical stimulus comes from the attending female. Additionally, the importance of the chemical communication between mother and tadpoles we detected here was expected, because chemical signals/cues are an efficient form of communication among animals in aquatic environments (Brönmark and Hansson 2000).

Contrary to our expectations, tadpoles seem to follow both familiar and unfamiliar attending females equally. However, we cannot assert whether tadpoles are unable to recognize their mothers or choose to follow any attending female due to advantages, such as a decrease in predation risk by following larger schools. Indeed, observations of

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schools of *L. podicipinus* mixing in the field was common, which eventually broke up into small schools to follow attending females performing pumping behaviour (JFCC, unpublished data). This fact may explain the frequency of schools with tadpoles at different developmental stages (see Supplementary 1). Thus, we hypothesize that tadpoles may benefit from receiving care and protection, increasing their chances of survival regardless of their genetic relatedness to the attending female. Among ectotherms, alloparenting (any parental care directed towards non-descendant offspring) is widely reported in fishes, ranging alloparental care of eggs to free-swimming juveniles (see Wisenden 1999). In anurans, alloparental care has been reported, at least, for centrolenids guarding egg clutches (Valencia-Aguilar et al. 2021) and *Leptodactylus* species with maternal care of tadpoles (Rodrigues et al. 2011). In the latter case, females were reported to attend interspecific mixed schools of *L. podicipinus* and *L. luctator* and intraspecific mixed schools of *L. luctator* (Rodrigues et al. 2011). Although alloparental care may reduce parental fitness (Trivers 1972; but see Wisenden 1999), in fishes, parents may benefit by one or more of the following mechanisms: mate acquisition, dilution effect, selfish herd effect, or differential predation effect (reviewed by Wisenden 1999). Our results suggest that tadpoles of *L. podicipinus* may benefit from unfamiliar female care, however, costs and benefits of alloparenting need to be addressed.

In free-swimming tadpoles, as in *Leptodactylus* species, the main function of parental care seems to be the protection of tadpoles against predators and guidance of schools to avoid deep waters, where predators are more abundant and food sources are limited (Vaz-Ferreira and Gerhau 1975; Martins 2001; Hurme 2015; Carrillo et al. 2023). Tadpoles and females travel long distances (see Wells and Bard 1988) and schools can follow the attending females even through channels and tunnels excavated by the mothers (Hoffmann 2006; Rodrigues et al. 2011). Thus, our experiments suggest, for *L. podicipinus*, that chemical communication plays an important role in these complex behaviours. Moreover, we observed that tadpoles respond to chemical compounds specifically produced by attending females, not by non-attending females or males. This suggests that attending females probably produce a chemical secretion to communicate with the tadpoles. In amphibians, chemical compounds are known to act as pheromones during courtship and territorial disputes (King et al. 2005; Starnberger et al. 2013). However, little is known about the compounds involved in chemical communication during parent-offspring interaction, which we are further investigating.

In conclusion, our research showed the importance of chemical stimulus in mother-tadpole communication in *L. podicipinus*, which significantly contributes to tadpole aggregation (schooling behaviour), and likely reduces predation risk. Additionally, the chemical secretion produced by attending females may contribute to tadpole attraction, facilitating female active defence of offspring (Carrillo et al. 2023). Our results also indicate that school attraction does not appear to be mother specific. Thus, tadpoles following unfamiliar attendant females are likely to benefit from alloparental care, as attending females appear unable to recognise related offspring. Finally, as many *Leptodactylus* species perform pumping behaviour (sensu Wells and Bard 1988; reviewed by Carrillo et al. 2023), the study of mother-offspring communication in other species will shed light on interesting gaps, including the identification of species-specific chemical compounds, the interaction among different signals/cues (e.g. chemical, tactile, visual), and the frequency and outcomes of alloparental care within this group of frogs with aquatic maternal care.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-024-03468-1.

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Author contributions JFCC, DJS and CPAP conceived and designed this study. JFCC conducted all experiments and analysed the data. JFCC, ZO, DJS and CPAP wrote this manuscript. All authors substantially edited and approved the final manuscript.

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Data availability All data generated or analyzed during this study are included in this published article.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval We captured the animals under SISBIO Brazilian License (68071-4). We conducted the experiments under bioethical approval of CEUA/UFMS from Universidade Federal de Mato Grosso do Sul, Brazil (ref. 1.085/2019). All applicable international, national, and/or institutional guidelines for the use of animals were followed.

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