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ORIGINAL PAPER

Acoustic underwater signals with a probable function during competitive feeding in a tadpole

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Abstract Acoustic communication is widespread among adult stages of terrestrial animals and fish and has also been observed in insect larvae. We report underwater acoustic communication in the larvae of a frog, *Gephyromantis azzurrae*, from Isalo, a sandstone massif in western Madagascar. According to our field data, these tadpoles live in streams and prefer habitats characterized by comparatively low temperatures, shallow water depth, and a relatively fast current. Feeding experiments indicated that the tadpoles are carnivorous and macrophagous. They consumed insect larvae and, to a lesser extent, small shrimps, and conspecific as well as heterospecific tadpoles. Calls of these tadpoles consisted either of single click notes or of irregular series of various clicks. Some complex calls have a pulsed structure with three to nine indistinct energy pulses. Production of the pulses coincided with rapid closure of the jaw sheaths and often with an upward movement of the body. Calls were emitted while attacking prey and occurred significantly more often when attacking conspecifics. Tadpoles that had not been fed for some time emitted sounds more frequently than those that had been regularly fed. The spectral frequency of the calls differed in tadpole groups of different size and was higher in groups of smaller tadpoles, suggesting that spectral frequency carries some information about tadpole size which might be important during competitive feeding to assess size and strength of competitors. This report differs from those for the larvae of South American horned frogs, *Ceratophrys ornata*. These are the only other tadpoles for which sound production has reliably been reported but the calls of *Ceratophrys* tadpoles occur mainly in a defensive context.

Keywords Amphibia · Mantellidae · *Gephyromantis azzurrae* · Tadpole · Sound production

Introduction

Acoustic communication is well established in non-aquatic vertebrates and insects. Birds use calls for courtship and territory delimitation (Podos et al. 2004), but acoustic communication also plays a prominent role in mammals, frogs, cicadas, and orthopterans (Wells 1977; Gerhardt 1994; Drosopoulos and Claridge 2006; Fitch 2006). Underwater acoustic communication is often less considered although a variety of fishes, marine mammals, and crustaceans emit sounds (Fish 1954; Hawkins 1993; Ladich 1997; Myrberg 1997; Popper et al. 2001; Ladich and Fine 2006).

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Whether in air or water, it is almost exclusively the adult stage that calls, although some caterpillars are known to emit clicking sounds to deter either predators or competitors (Yack et al. 2001; Brown et al. 2007). The developmental basis for acoustic communication in vertebrates traces back to early fishes and can be also observed in larval fishes (Bass et al. 2008); yet sound production in vertebrate larvae is virtually unknown.

In frogs, calls range from noisy and pulsed to tonal sounds (Duellman and Trueb 1986). Ultrasound communication is known in some species (Feng et al. 2006). Frog advertisement calls are usually species specific and genetically fixed without ontogenetic learning. They are typically composed of single or few stereotyped notes (Wells 1977; Ryan 1988; Cocroft and Ryan 1995; Narins et al. 2006), although some species emit a more extended call repertoire (Narins et al. 2000). Others have more complex bimodal types of communication that integrate visual with acoustic cues (Narins et al. 2005). Spectral frequency depends on body size, with larger frogs producing lower spectral frequencies. A number of temporal call variables (pulse rate, etc.) become slower at lower body temperatures (Gerhardt 1994).

In addition to diverse acoustic behaviors, frogs are also characterized by numerous reproductive strategies. Their typical larval stage is the tadpole, an aquatic, omnivorous suspension feeder with a highly derived morphology (Seale and Wassersug 1979; McDiarmid and Altig 1999; Altig et al. 2007). Multiple and convergent instances of terrestrial development and parental care are known (Duellman and Trueb 1986; Crump 1995), and several tadpoles have reversed to the probable ancestral feeding mode of tetrapod larvae by becoming carnivorous (Polis and Myers 1985; Ruibal and Thomas 1988; McDiarmid and Altig 1999; Grosjean et al. 2004).

Acoustic signaling had been reported for a tadpole from Madagascar belonging to the genus *Gephyromantis*, as a brief mention in a field guide (Glaw and Vences 1994). A brief description of sounds produced by tadpoles had much earlier been published by Vaz-Ferreira and Gehrau (1975) who observed sounds of about 6 kHz produced by groups of tadpoles of the South American *Leptodactylus ocellatus*, a species characterized by maternal care. Although it is compelling to assume a possible role of these sounds of *Leptodactylus* tadpoles for communication, either among shoaling tadpoles or between tadpoles and their mother, this hypothesis remains untested. More recently, Natale et al. (2010) provided compelling evidence for sound production in the carnivorous larvae of a South American frog, *Ceratophrys ornata.* These tadpoles emit a brief, clear, and very audible series of metallic-like notes when a conspecific tadpole attempts to prey upon it, or when touched by an object, probably to discourage predation, especially by conspecifics. Natale et al. (2010) speculated that other macrophagous carnivorous tadpoles may produce sounds as well.

Here we report more detailed data on the tadpole of *Gephyromantis azzurrae*, a frog of the Malagasy family Mantellidae, which had previously been observed to produce sounds (as *Gephyromantis corvus*; Glaw and Vences 1994). We demonstrate that this species is macrophagous and carnivorous, preying upon small aquatic arthropods, and regularly emits acoustic signals towards conspecifics. We hypothesize that this behavior probably represents aggressive signaling during competitive feeding and thus a new type of tadpole signaling behavior.

Materials and methods

Fieldwork and analysis of habitat variables

During March and April 2007, we sampled tadpoles in a total of 44 streams along 30-m transects per stream across the Isalo Massif. A variety of habitat variables were recorded (complete list of sites and details of sampling methods in SI). Multiple logistic regression was applied to identify habitat characteristics influencing the occurrence of *G. azzurrae* tadpoles. Twelve habitat variables were recorded along the transects to obtain an estimate of abiotic habitat characteristics influencing the occurrence of *G. azzurrae*: stream width and mean depth, stream proportion with fast and slow current, respectively, water temperature, pH, conductivity, and proportion of various types of substrate, i.e., organic matter (accumulation of dead leaves), sand, gravel, and rock. Water velocity in stream sections was categorized as “slow” in sections with almost stagnant water and as “fast” in parts of the stream with clear current. Measurements of temperature and water chemistry were instantaneous and were carried out on different days and randomly at different times of the day (not at night).

All tadpoles encountered during these surveys were identified by DNA barcoding (survey results and detailed morphological descriptions of tadpoles will be published elsewhere; for detailed survey methodology see Strauß et al. 2010). In Isalo, two very similar sibling species of *Gephyromantis* exist (Mercurio and Andreone 2007), *G. azzurrae* and *G. corvus*, both of which are characterized by tadpoles exhibiting roughly similar morphological specializations; both are probably carnivorous. Tadpoles assigned by DNA barcoding to *G. corvus* were very rare in our survey. They can be distinguished by a number of features of the oral disk and intensity of color pattern on tail. Tadpoles of *G. azzurrae* used for sound recordings and behavioral experiments were identified by their less intense tail pattern; they were obtained from streams in which no *G. corvus* tadpoles had been found.

Acoustic recording, observations on captive specimens, and statistics

A variety of experiments were carried out in February 2007 and 2008 on living, freshly caught tadpoles of *G. azzurrae* in Madagascar under largely natural conditions (water, substrates, prey from the original habitat). We defined small tadpoles (15–20 mm), medium-sized tadpoles (21–31 mm), and large tadpoles (35–44 mm total length). This definition of size classes followed a pragmatic approach, ensuring that the classes encompassed the smallest as well as the largest tadpoles present in the stream at the time of study, and that a sufficient number of individuals of each size class would be available for study. Tadpole calls and behavior were recorded in small tanks (16×3.5 cm, water depth 6.5 cm; water temperature 22–26°C) with a hydrophone (Avisoft Bioacoustics, TC4013) connected to a Marantz PMD670 digital recorder via an amplifier (Avisoft Bioacoustics, 48 V). A video camera (Sony DCR-SR30) was used to simultaneously record behavior. The internal microphone of the video camera also recorded the sounds which were amplified and emitted in real time via an external speaker connected to the digital recorder, ensuring synchronous recordings of sound and behavior. Spectral and temporal variables were analyzed using Cooledit 96 (Syntrillium) software. Spectrograms (=sonagrams) were produced using the package seewave (Sueur et al. 2008) in the R environment (R Development Core Team 2009). We compared calls among groups of differently sized tadpoles using parametric and non-parametric analyses of variance because correlation analyses were hampered by the impossibility of assigning a sound to a specific tadpole and thus to its exact body size. Statistical analysis was carried out using Statistica version 7 (StatSoft, Tulsa, OK) and R 2.9.0 (R Development Core Team 2009).

Behavior when confronted with different prey

Tadpoles for this and other experiments were collected in the Namazaha valley (Isalo National Park, Madagascar; 22° 53.883′ S; 45°37.575′ E; 772 m above sea level) on 6 February 2008. Specimens were reared in groups of ten in plastic containers of 32×32×13 cm. Commercial fish food (dried gammarid crustaceans) was provided and water exchanged daily.

Experiments were performed with tadpoles of *G. azzurrae* of 31–43 mm total length. Tadpoles were observed in 15-min experiments with four treatments. These were either confrontations with different types of potential prey or were controls, i.e., one tadpole was placed together with a small freshwater shrimp collected from water bodies in Isalo (15–16 mm total length), a tadpole of a different, sympatric frog species (*Boophis doulioti*; 24–26 mm total length), a conspecific tadpole of similar size (31–43 mm total length), or kept alone.

Per day, eight tadpoles were used in the experiments. Experiments were carried out over five days, thus with a total of 40 tadpoles. Each tadpole was used once in each of the four treatments. The evening before an experiment, each tadpole was kept alone in a small container (10×20×6 cm). The day of the experiment, the tadpoles were used four times in the same order for the experiments to ensure that the interval between experiments was similar for each individual. The order of experiments was randomized for each tadpole.

Behavior under different feeding regimes

The effect of the feeding state on aggressive behavior and calls of *G. azzurrae* was studied in February 2007 with tadpole specimens collected at Namazaha. These experiments followed a roughly similar design as those described in the previous section and carried out in 2008, but they were carried out independently and results of the two experiment series from 2007 and 2008 were kept completely separate for analysis. Each experiment lasted 15 min and was recorded using the same equipment as in 2008. In total, 118 experiments were carried out with tadpoles regularly fed with commercial aquarium fish food and 113 with tadpoles not fed for 72 h prior to the experiments. To assess intensity of attack behavior, experiments confronting tadpoles with shrimps, non-conspecific tadpoles and conspecific tadpoles were performed (same number of experiments per treatment carried out with fed and not fed tadpoles) and the results averaged (separately for each treatment) for fed vs. non-fed tadpoles. As the primary purpose of this experiment was to assess intensity of calling behavior under different feeding regimes, we averaged values over experiments with shrimps, non-conspecific and conspecific tadpoles, and controls and compared these averages between fed vs. non-fed tadpoles.

Substrate choice

Experiments were carried out in 32×32-cm containers with a randomized substrate divided in equal parts among dead leaves, sand, and gravel, with one tadpole per container. In 108 replicate experiments, we controlled the substrate chosen by the tadpole twice during daytime and twice at night; the results were averaged over all 432 observations.

Prey choice

For these experiments, we kept (in 2008) 20 tadpoles (total length ranging between 37 and 52 mm in total length) per treatment (a total of 100 tadpoles) for 48 h unfed and then transferred each into a tray of 10×20 cm (water depth 6 cm). Live prey were offered, either a smaller conspecific tadpole (total length in this experiment 17–19 mm), a slightly smaller conspecific tadpole (24–28 mm), a smaller *Boophis* tadpole (14–19 mm), a freshwater shrimp (10–16 mm), or a mayfly (Ephemeroptera) larva (5–10 mm). Experiments were run during 48 h, and every 2 h it was checked whether the prey had been eaten. For analysis, we compared numbers of different prey eaten after the full 48-h period.

Results

Ecology of *G. azzurrae* tadpoles at Isalo National Park

Of 44 streams surveyed in the Isalo region in February 2007, tadpoles of *G. azzurrae* (Fig. 1a, b) were found in 19 (incidence=43%). All of these were in canyons (*G. azzurrae* records in 11 out of 20 streams; 55%) and river valleys (eight out of 13; 62%) within the sandstone massif. We did not detect tadpoles in any of the three streams in the lowland forest or in the eight streams in savannah surrounding the massif. Multiple logistic regression (backward stepwise, $p=0.10$ for exclusion of variables, 20 iterations), starting with a model including all 12 variables, for the 33 localities within the massif only, identified low temperatures, shallow water depth, and a relatively fast water current as significantly predicting the presence of the species ($P<0.001$; Nagelkerke's $R^2=0.62$; Table 1).

Substrate choice

In substrate choice experiments, the tadpoles significantly (chi-square test, $P<0.05$, $n=108$) preferred dead leaves (61% of observations) over sand (24%) or gravel (15%).

Prey choice

Large tadpoles of *G. azzurrae* readily consumed a variety of different prey but showed the highest predation rate on insect larvae. Predation was low for small conspecific tadpoles (two consumed; 10%), medium-sized conspecific tadpoles (none consumed), small non-conspecific (*Boophis*) tadpoles (three consumed; 15%), and shrimps (two consumed; 10%). Predation was high for ephemeropteran larvae (19 consumed; 95%). One non-conspecific tadpole and two shrimps died in controls.

Tadpole calls

We recorded regular emission of distinct sounds from tadpoles of *G. azzurrae* to which we herein refer as calls. The basic unit, here referred to as note, is a short clicking sound of 8–24 ms in duration which in some cases shows a pulsed structure with three to nine indistinct energy pulses. Calls can consist either of single notes, or the notes can be arranged in distinct series. We here classify these alternative structures as two call types: simple versus complex calls. The frequency bandwidth is very large, and ranges from 2,000 up to at least 15,000 Hz (Fig. 1c); the dominant frequency is between 2,718 and 9,140 Hz, depending on the size of the specimens.

The number of calls was strongly different among groups of tadpoles of different size. We observed groups of five small, medium-sized, and large tadpoles for 30 min and averaged values over four replicates per treatment (original data in Table 2). Merging emission of simple and complex calls small tadpoles emitted on average 0.09, medium-sized tadpoles 0.49, and large tadpoles 1.01 calls per specimen per minute (total number of recorded calls $N=957$; Kruskal–Wallis ANOVA, $P<0.05$).

Dominant spectral frequency of calls also differed among tadpole size classes and revealed values of 6,654±1,126 Hz (4,125–9,140 Hz; $N=20$) for small tadpoles, 4,844±983 Hz (3,046–6,562 Hz; $N=20$) for medium-sized tadpoles, and 3,699±567 Hz (2,718–3,212 Hz; $N=20$) for large tadpoles (Kruskal–Wallis ANOVA, $P<0.001$).

Pulsed clicks were observed only in large tadpoles. Complex calls (series of three to five clicks) were only observed in large and medium-sized tadpoles, whereas small tadpoles only emitted simple calls or series of two clicks. No differences in note length were observed among size classes (data not shown). We could not directly observe the mechanism of sound production in these tadpoles due to their small size. Because the sound production is fast and usually associated with rapid movements of the tadpole, it was not possible to observe possible body contractions that might be indicative of the movement of an internal air stream, and we also did not observe any air bubbles expelled during the movement. However, at least for simple calls, our recordings provide evidence that the sound is produced during a rapid closure of the previously wide open jaw sheaths, often during an upward movement of the body (Fig. 1d). Although details are difficult to assess in our videos, during complex calls of two or three notes, each note corresponds to one opening of the mouth. Due to the scarcity of clear video recordings, we did not analyze whether the mouth opening in the context of sound production differs from typical movements during feeding and breathing.

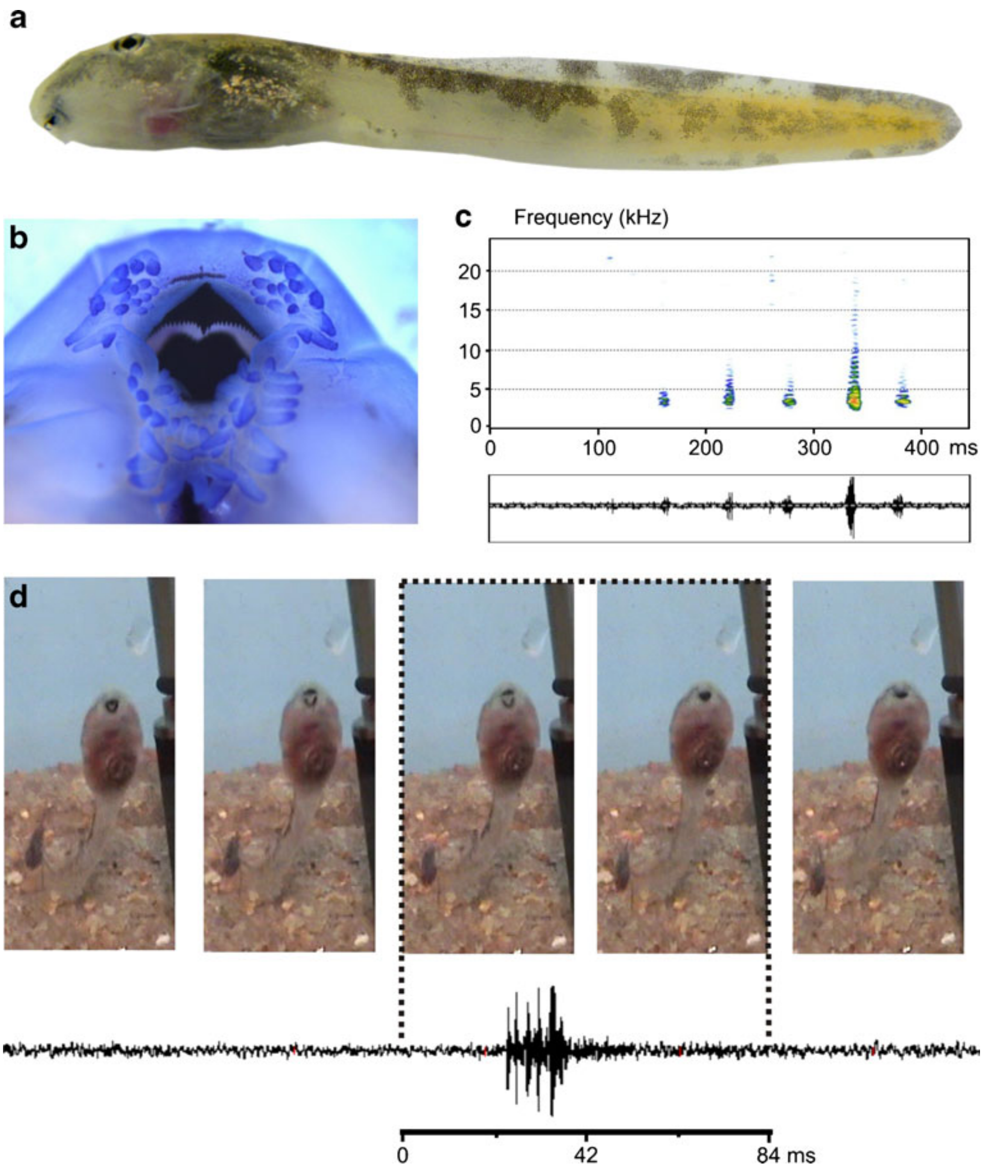

Fig. 1 The carnivorous tadpole of *G. azzurrae* **a** in lateral view and **b** its oral disk; **c** spectrogram and oscillogram of a complex call of the *G. azzurrae* tadpole (time scale in milliseconds), and **d** video frames (24 frames per second) and oscillogram of a simple call, showing that emission of sounds occurs simultaneously with the closing of the jaw sheaths

Factors influencing aggressive and acoustic behavior

Observations of large *G. azzurrae* tadpoles over 15 min ($N=40$ for all treatments) indicated that calls are regularly emitted by tadpoles kept alone, but much more frequent if kept together with prey or, especially, with other conspecific tadpoles (Fig. 2). Simple calls are more common than complex calls. They are often emitted in the context of an attack on the prey or attack on the other tadpole. However, they are emitted more frequently without such an attack. When the tadpole was disturbed or touched, it often emitted sounds as well. However, this behavior apparently typically occurred in the context of attacking the intruder rather than escaping since usually the tadpole turned around and emitted sounds while swimming towards and touching the intruder. Highly significant differences in aggressive and calling behavior were found with different prey types (Fig. 2). When the test tadpole was in the tank with a shrimp, attacks without calls (number of observed attacks per experiment, averaged over 40 replicated experiments 1.11) or with simple calls (1.43) were more common

Table 1 Final model for multiple logistic regression analysis after stepwise backward regression for 33 streams in the Isalo Massif area (canyons and river valleys). The initial model included 12 habitat variables as independent variables and the presence or absence of *G. azzurrae* tadpoles as dependent variable

Habitat variable	Regression coefficient
Mean water depth (cm)	−0.22
Temperature (°C)	−1.16
Proportion with fast current	0.27
Constant	29.97

The model was significant ($P<0.001$, $R^2=0.62$)

Table 2 Number of calls recorded from 30-min experiments in which five tadpoles were observed together in containers with about 3.2 cm^3 water per tadpole (for tadpole size classes, see main text)

Tadpole size class	*N* (single notes)	*N* (note series)
Large (group 1)	52	74
Large (group 2)	25	50
Large (group 3)	83	118
Large (group 4)	54	151
Medium sized (group 1)	20	35
Medium sized (group 2)	77	91
Medium sized (group 3)	21	24
Medium sized (group 4)	17	9
Small (group 1)	0	0
Small (group 2)	2	0
Small (group 3)	18	8
Small (group 4)	22	6

than with a conspecific (0.27/0.96) or non-conspecific (0.46/0.83) tadpole. In contrast, attacks with complex calls were more frequently observed with a non-conspecific (1.29) and especially with conspecific tadpole (2.73) than with a shrimp (0.63). Similarly, emission of complex calls without attack was highest with a conspecific tadpole (Fig. 2).

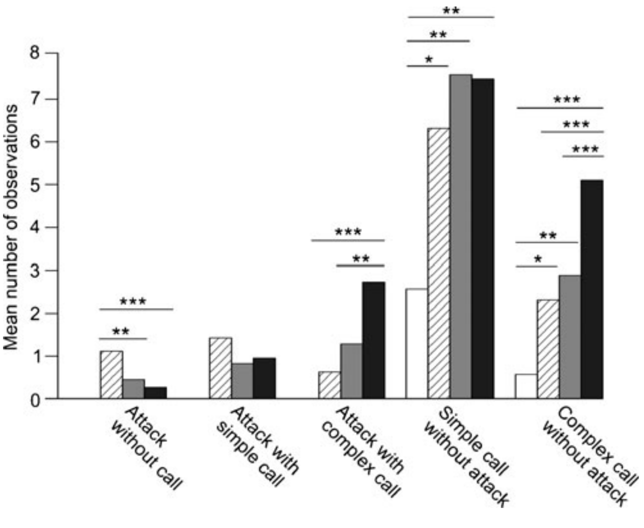

Fig. 2 Frequency of five types of aggressive and/or bioacoustic behavior by large tadpoles of *G. azzurrae* (31–43 mm) when kept during 15 min with either a freshwater shrimp (*hatched bars*), a tadpole of sympatric *B. doulioti* (*gray bars*), or a second *G. azzurrae* tadpole of similar size (*black*; total values reduced by 50% because calls of the two tadpoles could not be reliably distinguished). *White bars* are control treatments (*G. azzurrae* tadpoles kept alone). The *bars* indicate the average number of observations (attacks and/or calls) in 40 replicates per treatment. *Asterisks* indicate statistical significance of pairwise comparisons based on generalized linear models (Poisson distribution; *$P<0.05$, **$P<0.01$, ***$P<0.001$)

In an additional series of experiments (control, shrimp, non-conspecific, and conspecific tadpole treatments), tadpoles kept for 3 days without food performed three kinds of recorded aggressive behavior significantly more often than tadpoles that had been regularly fed (compared with *U* tests; Table 3). This applied to attacks with call ($P<0.001$), attacks without call ($P<0.05$), and calls without attack ($P<0.001$).

Further anecdotal experiments were documented as videos in Supplementary online material. In these a silicone tadpole model was suspended in front of a large tadpole of *G. azzurrae* (of similar size as the model). The tadpole did not flee when touched by it; instead, it turned around and attacked the model, emitting calls during this behavior. In some cases in which two tadpoles of similar size were kept together, intensive short fights with very fast calls were observed.

Discussion

Our data provide indications for a non-defensive acoustic communication system in an aquatic vertebrate larva. Tadpoles of *G. azzurrae* regularly emitted calls that we hypothesize are aggressive signals towards conspecifics during prey capture. A similar behavior is known from competitive feeding of fish (Amorim and Hawkins 2000; Amorim et al. 2004). The more complex type of call, a series of up to five pulsed notes (and in rare cases more), was emitted most frequently by tadpoles interacting with conspecifics, and only rarely during capture of invertebrate prey or attacks on tadpoles of other species. Furthermore, unfed tadpoles called significantly more often than fed specimens, indicating that aggressiveness and thus frequency of aggressive calls increase with hunger. As in adult frogs, the dominant frequency of the calls reflects the size of the specimens, which indicates that tadpoles may be able to assess the size and thus strength of a rival by its calls. Consequently, small tadpoles call less often and usually emit no note series. We hypothesize that this is because the probability that small tadpoles can impress their rivals by this putatively aggressive signal is lower, but we cannot exclude that sound production in young tadpoles is limited by an incomplete development of certain morphological characters.

Tadpoles of *G. azzurrae* are common in streams of the Isalo Massif and can occur at high densities. This prevents establishment and defense of feeding territories. The use of calls to defend well-delimited territories is thus unlikely, and is in disagreement with our observations of captive specimens that did not monopolize particular parts of the available space as would be the case in strictly defined territoriality. The available evidence supports instead a function during feeding, possibly to chase away conspecifics from possible food sources.

Table 3 Behavioral responses of *G. azzurrae* tadpoles during 15-min experiments, averaged over ca. 30 experiments per alternative treatments of adding a shrimp or a non-conspecific tadpole as food, or a conspecific tadpole, repeated for regularly fed tadpoles and tadpoles unfed for 72 h

Treatment	Fed	Non-fed
Attacks with calls***	1.2±1.2 (0–11), *n*=88	3.1±2.8 (0–11), *n*=83
Attacks without calls*	1.7±2.3 (0–14), *n*=88	2.9±3.8 (0–19), *n*=83
Calls without attack***	0.9±1.6 (0–9), *n*=118	3.8±5.3 (0–28), *n*=113

Results were averaged over all treatments (controls considered only for calls without attack)

$^*P<0.05$, $^{***}P<0.001$

The context of sound production in the tadpoles of *G. azzurrae* differs distinctly from that in the similarly macrophagous and carnivorous larvae of *Ceratophrys ornata*. The larvae of this South American frog do not produce sounds during the whole sequence of attack (Natale et al. 2010). Instead they emit a brief metallic-like sound when touched or bitten by a conspecific larva, or touched by an object. Hence, there is evidence for a defensive function of the calls of *Ceratophrys* tadpoles, whereas the calls of *G. azzurrae* tadpoles probably are predominantly aggressive. To test this hypothesis, experimental evidence is needed to understand (both in *Ceratophrys* and *Gephyromantis*) if these tadpoles are able to hear the conspecific calls and to react accordingly. Are attacking *Ceratophrys* tadpoles less likely to kill or injure a calling tadpole compared to a non-calling one? Are *G. azzurrae* tadpoles more likely to escape over short distances if attacked or touched in conjunction with a call? These crucial pieces of evidence for understanding the acoustic communication systems in these tadpoles are so far missing.

The tadpoles of *G. azzurrae* are characterized by an orange color of their tails (Fig. 1a) that is exceptional among other Malagasy anuran larvae, most of which are stream dwelling and occur in species-rich communities (Strauß et al. 2010). This color pattern so far has only been observed in three species of *Gephyromantis* (subgenus *Phylacomantis*), i.e., *G. azzurrae* and *G. corvus* (this paper) and *G. pseudoasper* (Randrianiaina et al. 2007). We here speculate that it may serve as a visual cue to recognize conspecifics and confers some kind of (possibly aggressive) signal, although this hypothesis remains untested. Similar tadpole morphologies are found in several additional *Gephyromantis* species which together with *G. azzurrae* form a monophyletic group, the subgenus *Phylacomantis* (Glaw and Vences 2006). Although some *Gephyromantis* have generalized tadpoles, others have derived reproductive modes, with either direct development, non-feeding tadpoles, or (in *Phylacomantis*) carnivorous and sound-emitting tadpoles (Randrianiaina et al. 2007). The evolutionary origins of this larval diversity cannot at present be deciphered because the available phylogenies (e.g., Glaw and Vences 2006) do not reliably resolve the relationships among the various *Gephyromantis* lineages.

The calls recorded for tadpoles of *Ceratophrys ornata* are very similar to the distress calls (as defined by Duellman and Trueb 1986) emitted by recently metamorphosed froglets of the same species but different from those of adults (Natale et al. 2010). Because (1) early stage larvae of this species have lungs, a soft-tissue open glottis, and a pair of laryngeal muscles, (2) temporal call variables are positively and spectral call frequency negatively associated with body size, and (3) sound production is increased in specimens removed from water, it is likely that their sound production is related to the movement of atmospheric air from the lungs through the glottis (Natale et al. 2010).

The calls of *Ceratophrys* tadpoles by general impression strongly resemble those of the tadpoles of *G. azzurrae*, and various temporal and spectral parameters of the tadpole calls of the two species are roughly similar. Also, the spectral frequency of tadpole calls of *G. azzurrae* appears to decrease with body size, similar to what has been demonstrated in *Ceratophrys*. This indicates that sound production in the two species might be similar, i.e., by the movement of air from the lungs through the glottis. However, it is remarkable that the general sound type of *G. azzurrae* tadpoles also agrees with the observations in clownfish of the genus *Amphiprion* in which sound results from the collisions of the jaw teeth, transferring energy to the jaws that are presumably the sound radiator (Parmentier et al. 2007). Our data demonstrate that sounds are produced by *G. azzurrae* tadpoles while closing the massive jaw sheaths that may produce sounds by friction of their serrations (Fig. 1b). Detailed morphological examinations and real-time microtomographic recordings (Westneat et al. 2008) are necessary to elucidate whether the sounds of *G. azzurrae* are produced by moving air from the lungs through the glottis or, roughly similar to *Amphiprion*, might result from collision of and friction between serrations of jaw sheaths, or even by a mechanism based on implosion of air into rapidly opening air chambers as in most of the aquatic tongueless frogs in the family Pipidae (Yager 1992).

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