

## Simulated chorus attracts conspecific and heterospecific Amazonian explosive breeding frogs

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### Abstract :

In tropical regions, some anuran species breed "explosively", reproducing in massive and highly diverse aggregations during a brief window of time. These aggregations can serve as acoustic beacons, attracting other anurans toward seasonal ponds. We hypothesize that conspecific and heterospecific calls play a role in navigation toward ponds and synchronization of reproduction among species. We simulated a chorus of two species (*Trachycephalus coriaceus* and *Chiasmocleis shudikarensis*) with contrasting call characteristics (low-frequency vs. high-frequency) and reproductive strategies (strict pond breeder vs. opportunistic) near known explosive breeding sites. We predicted that choruses of *T. coriaceus* are more attractive to heterospecifics than of *C. shudikarensis* because the first provides a more reliable indicator of a suitable breeding pond and a better long-distance signal. We found that both choruses attracted conspecific frogs to the playback outside a natural breeding event. As predicted, heterospecifics were attracted only by low-frequency calls of *T. coriaceus* that breeds exclusively in large ponds, but not by higher frequency calls of *C. shudikarensis* that also breeds in small pools not suitable for other species. Our study presents the first experimental evidence that tropical explosive breeding anurans are attracted to conspecific and heterospecific choruses. The contrasting effect of the playback of the two species on heterospecifics suggests that the attractive effect of a chorus depends on the reproductive strategy of both the sender and the receiver. Given the abundance and diversity of communities in tropical ecosystems, the use of heterospecific acoustic cues may prove widespread and requires further investigation. Abstract in Portuguese is available with online material.

**Keywords :** Anuran, French Guiana, Neotropics, orientation, phonotaxis, reproduction

## 51 1. INTRODUCTION

52  
53 Social information obtained from conspecifics, and sometimes from heterospecifics, can be used  
54 by animals to assess the presence of resources or threats (Danchin *et al.* 2004; Goodale *et al.*  
55 2010). Animals forming mixed-species breeding aggregations, such as some birds (Monkkonen *et*  
56 *al.* 1999; Thomson *et al.* 2003; Mukhin *et al.* 2004), mammals (McGuire *et al.* 2009; Forsman *et*  
57 *al.* 2012) and amphibians (Diego-Rasilla & Luengo 2004, 2007; Pupin *et al.* 2007; Madden &  
58 Jehle 2017) can rely on the presence of others that share their habitat requirements to orientate  
59 themselves towards these habitats and the information they use can be acoustic (e.g. Magrath *et*  
60 *al.* 2005; Phelps *et al.* 2007).

61 Most anuran amphibians (i.e., frogs and toads) need water for breeding, and the ability to  
62 orientate and migrate toward aquatic sites is crucial for survival and reproduction (Wells 2007;  
63 Pittman *et al.* 2014; Sinsch 2014; Joly 2019). Depending on species and the context, amphibians  
64 can use acoustic, magnetic, mechanical, olfactory, and visual directional information (for reviews  
65 see Ferguson 1971; Sinsch 1990; 2006). Natal imprinting and spatial memory play a crucial role  
66 when returning to known oviposition sites (e.g., Heusser 1960; Shoop 1965; Ishii *et al.* 1995;  
67 Pašukonis *et al.* 2016), but social cues are also particularly important when locating new  
68 resources, facilitating orientation, and synchronizing breeding activity (e.g., Stamps 1988; Reed  
69 *et al.* 1993; Seppänen *et al.* 2007; Buxton *et al.* 2015; 2018; James *et al.* 2015). Acoustic  
70 communication, in particular, plays a key role in the reproductive biology of anuran amphibians  
71 (Gerhardt & Huber 2002), and male choruses could represent a cue indicating suitable breeding  
72 habitat.

73 Despite the fact that most amphibians occur in the tropics (Jenkins *et al.* 2013),  
74 experimental studies on cues guiding amphibians to breeding ponds remains limited to only a few  
75 temperate-region species. These studies have shown that some but not all anurans are attracted to

76 conspecific chorus (e.g., Gerhardt & Klump 1988; Ryan *et al.* 1981; Wollerman 2002; Bee 2007;  
77 Swanson *et al.* 2007; Christie *et al.* 2010; Buxton *et al.* 2015; 2018; James *et al.* 2015; Chang *et*  
78 *al.* 2018). Current evidence suggests that species which depend on unpredictable seasonal ponds  
79 are more attracted to conspecific playback than species that rely on stable, permanent ponds  
80 (Gerhardt & Klum 1988; Buxton *et al.* 2015; 2018 but see Swanson *et al.* 2007). In addition,  
81 acoustic cues of sympatric anurans might be used by newts to orientate toward shared breeding  
82 sites (Diego-Rasilla & Luengo 2004, 2007; Pupin *et al.* 2007; Madden & Jehle 2017 but see  
83 Slabbekoorn & Bouton 2008). Such heterospecific phonotaxis has also been suggested for  
84 anurans although direct evidence remains limited, especially under natural conditions (Oldham &  
85 Gerhardt 1975, Gerhardt & Klump 1988; Ryan & Rand 1993, Bernal *et al.* 2007). Chang *et al.*  
86 (2018) recently used a naturalistic setup to demonstrate that males of a tropical treefrog  
87 (*Rhacophorus prasinatus*) approach a chorus of some heterospecific frogs but ignore other  
88 sympatric species. Such selective use of heterospecific cues may reflect cost/benefit trade-offs of  
89 interspecific interaction requiring further investigation.

90         Some anuran species ‘explosively breed’ (sensu Wells 1977), aggregating in groups  
91 numbering hundreds to thousands of individuals and call during a narrow time window of just a  
92 few hours or days per breeding season. An explosive breeding strategy may be beneficial, by  
93 diluting the predation risk for adults, eggs, and larvae and increase mate attraction (Ryan *et al.*  
94 1981; Gerhardt & Huber 2002). In tropical regions such as Amazonia, anuran explosive breeding  
95 generally involves highly-diverse communities with sometimes more than ten species breeding  
96 simultaneously (Aichinger 1987; Hödl 1990; Gottsberger & Gruber 2004; Prado *et al.* 2005;  
97 Ulloa *et al.* 2019). Such phenomena typically occur in ephemeral sparsely distributed ponds  
98 (Rodrigues *et al.* 2010) that dry out during periods of low precipitation and thus have relatively  
99 few aquatic predators when ponds fill up during the rainy reason. Explosive breeding events are  
100 so localized, brief and synchronized that the yet largely unknown cues triggering these events

101 must be spatiotemporally unequivocal across species. Ulloa *et al.* (2019) found that rainfall  
102 during the previous 48 hours was the most important factor predicting explosive breeding events  
103 in French Guiana, which could also trigger the long distance migration of individuals with  
104 previous experience of the breeding sites. However, such environmental triggers are unlikely to  
105 explain how dispersers locate new distant breeding sites and how they synchronize their  
106 migration for arrival into the pond. The acoustic intensity of the choruses can reach 100 dB SPL  
107 measured in the middle of the aggregation and can be heard several hundreds of meters away.  
108 We, therefore, hypothesize that intense chorus sound is used by tropical explosive breeding  
109 species to both synchronize breeding among species and to orientate toward breeding sites.

110         To test if calls of explosively breeding frogs are attractive to both conspecifics and  
111 heterospecifics, we carried out a field playback experiment near known explosive breeding sites  
112 in the Amazonian rainforest of French Guiana. We specifically tested whether the chorus  
113 produced by two common explosive breeder species with divergent call characteristics and life-  
114 histories can attract conspecifics and heterospecifics outside a natural explosive breeding event.  
115 The first species, *Trachycephalus coriaceus*, is a large arboreal frog that breeds exclusively in  
116 large ephemeral ponds that are suitable for numerous other species of explosive breeders. Thus, *T.*  
117 *coriaceus* calls may be used as a reliable acoustic cue indicating suitable breeding habitat by  
118 other species. The second species, *Chiasmocleis shudikarensis* is a small terrestrial frog that also  
119 uses smaller ephemeral ponds not suitable for other species. Thus, their calls may not be a  
120 reliable cue for heterospecifics. If explosive breeders are selectively using social information,  
121 then we predict *T. coriaceus* choruses to attract both heterospecifics and conspecifics, and *C.*  
122 *shudikarensis* choruses to only attract conspecifics.

123

## 124 **2. MATERIALS AND METHODS**

125

126 **2.1. Study site**

127  
128 Experiments were carried out in three temporary ponds in French Guiana, along the Kaw  
129 Mountain (4°36'N; 52°16'W) where explosive breeding events have been irregularly surveyed for  
130 the last 15 years (Figure 1A). The climate is characterized by two periods of rainfall: the small  
131 rainy season takes place from early December to the end of February while the main rainy season  
132 occurs from April to July. Temporary shallow water bodies, or ponds, are flooded during the rainy  
133 seasons and then dry out during periods of low rainfall. The study sites corresponded to three  
134 temporary ponds named “Blanc”, “Arlesienne” and “Caiman”. These ponds are surrounded by  
135 dense tropical forest, located between 236 and 313 m above sea level, covering an area of 399.5  
136 m<sup>2</sup>, 672.0 m<sup>2</sup> and 1192.3 m<sup>2</sup> respectively.

137

138 **2.2. Playback experiment**

139

140 Four diamond-shaped pitfall stations were deployed at the onset of the rainy season 40 m away  
141 from each pond (Figure 1B). Fourteen litre buckets linked with 70 cm high plastic tarp fences  
142 were used to trap anurans. Three out of four of pitfall stations were equipped with a speaker (Fun  
143 Generation PL 108 A) powered by a generator (Honda EU1000i operating at 50 dB A) placed  
144 near the pond i.e. at a similar distance from all the pitfall stations. The fourth pitfall station was  
145 used as a silent control to estimate the number of anurans captured accidentally in the area.

146 We used three different playback stimuli: (1) *Chiasmocleis shudikarensis*, (2)  
147 *Trachycephalus coriaceus*, and (3) pink noise – a random noise having equal energy per octave  
148 similar to the background noise of rainfall (Figure 2). These stimuli were built using Logic pro  
149 one (Apple inc.). *Chiasmocleis shudikarensis* emits a continuous series of multipulsed notes (17  
150 fused pulses per note) of 0.095-0.099 s in duration and spaced by 0.065-0.010 s pauses. The

151 fundamental frequency ( $f_0$ ) is at about 1.6 kHz with a positive frequency modulation of about 0.5  
152 kHz from the beginning to the end of each note. The dominant frequency, which corresponds to  
153 the second harmonic ( $2f_0$ ), is at about 3.5-3.6 kHz. The *C. shudikarensis* stimulus consisted of a  
154 42 s recording of an isolated individual of *C. shudikarensis* (Marty & Gaucher 1999), copied 100  
155 times within a single track, each copy being successively time-shifted of 0.5 s (Fig. 2B).  
156 *Trachycephalus coriaceus* emits long moans of 0.9-1 s in duration irregularly spaced every  
157 second or so. These calls are trains of pulses (60 / s) with a fundamental frequency ( $f_0$ ) around  
158 0.35 kHz. The fundamental frequency is the dominant frequency (Fig. 2A). The *T. coriaceus*  
159 stimulus consisted of a 52 s recording of a chorus of five individuals of *T. coriaceus* (recorded by  
160 Thomas Tilly), copied five times within a single track, each copy being successively time-shifted  
161 being successively time-shifted of 0.5 s (Fig. 2B). For this track, sounds of frequency above 1  
162 kHz, corresponding to other surrounding species, were removed using a high-pass filter. The time  
163 shifting process produces a continuous chorus of overlapping calls that mimics a chorus  
164 sequence, and the number of overlapping tracks approximates the abundance of individuals  
165 generally observed in the ponds ( $\sim 100$  *C. shudikarensis* and  $\sim 25$  *T. coriaceus*). The pink noise  
166 was generated by an internal function generator of LogicPro (Fig. 2B). These sequences were  
167 looped in order to last the duration of the playback. All sounds had a sampling frequency of 44.1  
168 kHz and digitization depth of 16 bits.

169         The playbacks were carried out simultaneously for six successive nights at each pond  
170 from 2 to 7 December 2018, seven days after the reproduction of the explosive breeding species.  
171 Each station was playing one of the three stimuli between 1900 h and 2200 h. No specimens were  
172 found in the pitfalls before each playback. The acoustic level (peak measurement) of the  
173 playbacks was measured at a 1 m distance from the speaker at waist height. The level was set at  
174 95 dB SPL at 1 m, which corresponded to measurements taken in the same ponds during previous  
175 explosive breeding events (AF personal observation). To avoid any spatial habituation, the three

176 stimulus tracks were rotated clockwise between the pitfall stations each night. After 1h30 of  
177 playback (that is, at 2030 h), all frogs were counted in the pitfalls, in the trees surrounding each  
178 station within the limit of the plastic tarp fences, and on the ground within the same limits (4.5m  
179 radius = ~60 m<sup>2</sup>). A second count was made at the end of the playback session (that is, at 2200 h).  
180 Because counted individuals were neither caught nor marked during the playback, only the  
181 results of one counting session (that with the highest number of individual frog counts) was used  
182 for the analysis. For the same reason the sex of the individuals could not be recorded. The  
183 animals were released near the pond, about 5 m away from the fence at the end of the playback.  
184 One speaker of the “Blanc” pond failed to play back the pink noise before the second night. No  
185 calling activity of the observed species was heard during the experiment.

186

### 187 **2.3. Data analysis**

188

189 A generalized linear mixed-effects model (GLMM) was used to test whether the number of  
190 individuals found around the playback speaker was influenced by the acoustic stimuli. The  
191 number of individuals was combined over the three ponds and included individuals found in  
192 ground pitfalls (terrestrial species) and on tree branches (arboreal species). The model included  
193 the acoustic stimuli and the species as fixed effects, and date and pond as random effects. The  
194 model was fitted in R (R core Team 2019) using the function `glmer` of the R-package `lme4` (Bates  
195 *et al.* 2014). Since the response variable is a count variable, a Poisson GLMM was first fitted, but  
196 the dispersion statistic of the fitted model indicated a slight overdispersion ( $\hat{c}=2.67$ ). Hence,  
197 the next model in complexity was fitted with a negative binomial GLMM (Lindén and  
198 Mäntyniemi 2011). The Akaike information criterion (AIC; Akaike 1973) computed on both  
199 models (the Poisson and the negative binomial models), indicated that the negative binomial  
200 model was more suitable. Model stability was checked by excluding ponds and dates, one at a

201 time, from the data. This check did not indicate any influential ponds or dates. Variance Inflation  
202 Factors were derived using the function `vif` of the R-package `car` (Fox & Weisberg 2011). When  
203 applied to a standard generalized linear model excluding the random effects, it did not indicate  
204 collinearity to be an issue. The fitted model was not zero-inflated as revealed with the function  
205 ‘`testZeroInflation`’ from the R-package `DHARMA` (Hartig 2017). The full model was compared  
206 with the null model (including only the species and the random effects, pond and date) with a  
207 likelihood ratio test using the base R function ‘`anova`’, with argument `test` set to ‘`Chisq`’.

208           To compare the counts of each species, two additional models were fitted, one for *C.*  
209 *shudikarensis* and one for *T. coriaceus*. Since the counts for *O. leprieurii* were zero on three of  
210 the four experiments, no model was fitted for this species. As for the previous analysis, model  
211 stability and the absence of zero inflation were checked. Then, a Tukey test was performed as a  
212 post-hoc procedure to examine pairwise comparisons for each species between treatments. The  
213 post-hoc test was computed with the function ‘`glht`’ from the R package `multcomp` (Hothorn *et al.*  
214 2008).

215           The data that support our findings are openly available in Dryad at  
216 <https://doi.org/10.5061/dryad.8w9ghx3jr>.

217

### 218 **3. RESULTS**

219

220 We observed a total of fourteen species around the playback stations. Among these fourteen  
221 species, six were explosive breeding species (see below), five were prolonged arboreal breeding  
222 species (*Dendropsophus minutus*, *D. sp. 1*, *Callimedusa tomopterna*, *Phyllomedusa vaillanti*,  
223 *Scinax sp. 2*) and four were terrestrial breeding species (*Adenomera andreae*, *Rhinella*  
224 *castaneotica*, *Leptodactylus mystaceus*). Out of these fourteen species, only six were detected in  
225 the pitfalls (*Chiasmocleis shudikarensis*, *Trachycephalus coriaceus*, *Osteocephalus leprieurii*, *R.*

226 *castaneotica*, *Ceratophrys cornuta*, *A. andreae*). Among the explosive breeding species, half  
227 were detected in too low numbers (< 6 individuals) to draw any conclusion (*O. taurinus*, *C.*  
228 *cornuta*, *Scinax* sp. 3). However, males and females belonging to three species (*C. shudikarensis*,  
229 *T. coriaceus* and *O. leprieurii*) were found frequently at playback stations. None were observed  
230 calling, but *T. coriaceus* were observed in amplexus on two occasions, and *O. leprieurii* on one  
231 occasion.

232 Overall, the full GLMM was significant compared to the null model ( $\chi^2=49.71$ ,  $df=3$ ,  
233  $p<0.001$ ), revealing that there was a clear effect of the acoustic stimuli and species on the  
234 probability of attracting individuals using the playback. More specifically, the stimulus "*T.*  
235 *coriaceus*" had the stronger effect in attracting individuals when compared with the other stimuli.  
236 The stimuli "*C. shudikarensis*" and pink noise also had a positive effect of attracting individuals,  
237 however the pink noise stimulus was not significant (Table 2).

238 Post-hoc test on the species *C. shudikarensis* revealed significant differences between the  
239 silent and the "*C. shudikarensis*" stimuli ( $x= 1.3218$ ,  $p<0.01$ ), and between the silent and "*T.*  
240 *coriaceus*" stimuli ( $x=1.1802$ ,  $p=0.032$ ). Differences between the silent and pink stimuli were not  
241 significant. For the species *T. coriaceus*, the post-hoc test revealed a significant difference  
242 between the silent and "*T. coriaceus*" stimuli ( $x= 4.2195$ ,  $p<0.001$ ) and between the pink and the  
243 "*T. coriaceus*" stimuli ( $x=2.5078$ ,  $p<0.001$ ). "*C. shudikarensis*" stimulus for *T. coriaceus* was not  
244 analyzed statistically since it only had zero values. It is noteworthy that *O. leprieurii* were only  
245 found with the "*T. coriaceus*" playback. *Osteocephalus taurinus*, *Ceratophrys cornuta* and *Scinax*  
246 sp. 3 was also attracted by the "*T. coriaceus*" track and the pink noise and but unfrequently and in  
247 low numbers.

248

#### 249 **4. DISCUSSION**

250

251 Our study presents the first experimental evidence that tropical explosive breeding anurans are  
252 attracted to conspecific and heterospecific choruses. As expected, males and females of  
253 *Chiasmocleis shudikarensis* and *Trachycephalus coriaceus* were attracted to conspecific calls.  
254 Moreover, the call of *T. coriaceus* also attracted heterospecific *C. shudikarensis* and  
255 *Osteocephalus leprieurii* as well as other species in low numbers. The traps used were not set  
256 within natural breeding sites but were still effective at attracting a number of explosive breeding  
257 anuran species, suggesting that explosive breeders use heterospecific calls to locate new breeding  
258 sites and synchronize their reproduction.

259 A variety of animals use heterospecific cues and signals as ‘public information’, through  
260 which they are able to assess the presence of resources or potential risks (Goodale *et al.* 2010).  
261 For example, male túngara frogs, *Engystomops pustulosus*, adjust their calling behaviour to the  
262 calls of other species - probably as an indicator of predation risk (Phelps *et al.* 2007). Many  
263 migrating species rely on the presence of heterospecifics that share their habitat requirements to  
264 orientate themselves towards these habitats, a pattern that occurs in marine crustaceans (Stanley  
265 *et al.* 2012), marine molluscs (Lillis *et al.* 2013), marine fish (Simpson *et al.* 2005), birds  
266 (Mukhin *et al.* 2004; Thomson *et al.* 2004), frogs (Chang *et al.* 2018) and newts (Diego-Rasilla &  
267 Luengo 2004; Pupin *et al.* 2007, Madden & Jehle 2017). Our study suggests that such ‘public  
268 information’ produced by male mating calls may also play a role in the breeding ecology of  
269 tropical explosively breeding frogs.

270 As predicted, only the vocalization of *Trachycephalus coriaceus*, but not those of  
271 *Chiasmocleis shudikarensis*, attracted other species. Being an exclusively explosive breeder and  
272 arboreal, *T. coriaceus* might be able to detect the accumulation of water faster than other species  
273 and trigger the migration of other conspecifics and heterospecifics toward ponds of sufficient  
274 size. Individuals of *T. coriaceus* were observed at the speaker only a few minutes after the start of  
275 the playback, even though the natural explosive breeding had occurred days before the

276 experiment. This observation suggests high mobility and opportunistic readiness of this species to  
277 reproduce. The call of *T. coriaceus* is also notably lower in frequency compared to other  
278 explosive breeding species (Ulloa *et al.* 2019). Low frequency sounds propagate further than  
279 higher frequency sounds in dense habitats (Larsen & Radford 2018), making the calls of *T.*  
280 *coriaceus* a more suitable long-distance cue for other species. In contrast, the calls of *C.*  
281 *shudikarensis* did not attract heterospecific frogs suggesting that this species does not play a role  
282 in the emergence of explosive breeding events. The call of this species might not be a reliable cue  
283 since *C. shudikarensis* is a small-bodied opportunistic breeder that also calls from small puddles  
284 that are not suitable for larger species. The differential effects of the calls of these two species on  
285 heterospecifics suggests that the attractive effect of a chorus depends both on the reproductive  
286 strategy of the sender and the receiver, as recently shown in another tropical treefrog (Chang *et*  
287 *al.* 2018). Nevertheless, an experiment in a controlled environment would be needed to tease  
288 apart detectability and ecological relevance of heterospecific cues.

289         The anuran peripheral auditory system display enhanced sensitivity to frequency range of  
290 conspecific calls (Simmons 2013). Tuning of the auditory perception is particularly expected in  
291 environments with high levels of social background noise, the “cocktail party problem”, such as  
292 those experienced by explosive breeding frogs (Velez *et al.* 2013). In the absence of data on the  
293 auditory perception of the species involved in our experimentation, we cannot rule out that the  
294 higher frequency of the *C. shudikarensis* stimulus (3.6 kHz) was simply not perceived by  
295 *Trachycephalus coriaceus* and *Osteocephalus leprieurii* which emit lower dominant frequencies  
296 about 0.3 and 1.6 kHz respectively. Nevertheless, even if tuned toward conspecific frequency,  
297 frogs most likely remain able to perceive a wide bandwidth from their environment such as rain  
298 and fire (Grafe *et al.* 2002, Penna *et al.* 2005) but also heterospecific individuals (Gerhardt &  
299 Schwartz 1995).

300            Suitable breeding sites are often patchy and limited for anuran species, and several studies  
301 have demonstrated that conspecific choruses allow frogs to locate ponds (e.g. Gerhardt & Klump  
302 1988; Bee 2007; Buxton *et al.* 2015; 2018; James *et al.* 2015; Chang *et al.* 2018). The use of  
303 acoustic cues presumably increases the chance of encountering mates and helps in searching for a  
304 suitable habitat while minimizing energetic expenditure. Since mixed-specific choruses are  
305 common in the tropics, heterospecific calls could often be used as indicators of suitable breeding  
306 sites. Moreover, the calls of the species in the explosive breeding community vary greatly in call  
307 intensity. Some species produce relatively loud calls (e.g., *C. cornuta*, *T. coriaceus*) but other,  
308 such as *O. lepreurii* and *Scinax* spp., individually call at much lower intensities. The ability of  
309 the later to use loud heterospecific calls may allow them to find breeding sites and provide a  
310 timing cue without having to invest energy and exposing themselves to the risks related to loud  
311 conspicuous calls. In this context, lower intensity calls may have either been selected for  
312 heterospecific phonotaxis, or were the consequence of selection for minimizing energy  
313 expenditure when heterospecific calls can be used to find the breeding sites. If multiple anuran  
314 species rely on the calls of only a few species (such as *T. coriaceus*) to find suitable breeding  
315 sites, then this would also suggest they could represent keystone species for the explosive  
316 breeding community.

317            Anurans with prolonged breeding seasons typically face strong competition for food  
318 availability, calling territories, oviposition sites, and acoustic space with conspecifics and  
319 heterospecifics (Robertson 1986; Wogel *et al.* 2006; Wells 2007; Amézquita *et al.* 2011; Chang *et*  
320 *al.* 2018). These species show a variety of derived reproductive strategies, such as terrestrial  
321 oviposition and parental care, and males may avoid overcrowded breeding sites investing instead  
322 in searching for suitable long-term territories (Wells 1977; Duellman & Trueb 1994; Wells 2007).  
323 In contrast, explosive breeding events occur very rapidly and gather multiple species, all  
324 depositing eggs directly in the water suggesting limited competition for food, territory,

325 oviposition sites, and acoustic space; the benefits seem to outweigh the cost of intra- and  
326 interspecific competition. Competition among larvae is poorly understood, but distinct  
327 ecomorphological guilds (e.g. suspension feeder, nektonic, benthic) (Altig & Johnston 1989;  
328 Schulze *et al.* 2015) and niche partitioning might limit competition among heterospecific larvae  
329 (Inger *et al.* 1986; Alford 1999). Moreover, the benefits of explosive breeding system have been  
330 claimed to depend on the dilution effect toward predators favouring large aggregations (Wrona &  
331 Dixon 1991). Explosive breeding is thus particularly favourable to the emergence of  
332 heterospecific interactions. Heterospecific audiences could be beneficial to loud callers because  
333 the increased number of individuals decreases the predation risk per individual. Therefore, the  
334 trade-off between increased competition and the predator dilution effect might favour the co-  
335 evolution of heterospecific eavesdropping in explosive breeders.

336         Heterospecific eavesdropping is widespread across animals (Goodale *et al.* 2010), but the  
337 empirical evidence of acoustic interactions among amphibian species is scarce and limited to  
338 prolonged breeders and species assemblages with low diversity (e.g. Diego-Rasilla & Luengo  
339 2004, 2007; Pupin *et al.* 2007; Madden & Jehle 2017; Chang *et al.* 2018). Our study shows that  
340 tropical explosive breeding anurans are attracted to heterospecific acoustic signals that indicate a  
341 potential breeding opportunity, which is extremely circumscribed in space and time. Given the  
342 abundance and diversity of communities in tropical ecosystems, the use of heterospecific acoustic  
343 cues could prove to be widespread and requires further investigation. Moreover, the use of  
344 conspecific signals to attract animals to suitable habitats is a management strategy used for birds  
345 and frogs (Buxton *et al.* 2015; 2018). Our results suggest that in tropical systems, playbacks of  
346 the calls of certain species could be used in a conservation context at a community scale.

347

348 Table 1: Mean number of individuals per stimulus (*C. shudikarensis*, *T. coriaceus*, pink noise,  
 349 silent) averaged over six nights, and over the three ponds. The three most abundant species are  
 350 underlined in grey, and the explosive breeding species are in bold (the other ones are prolonged  
 351 breeder; *A. andreae* and *R. castaneotica* do not breed in the pond).  
 352

Stimulus	Mean number of individuals per night/pond				Total
	<i>C. shudikarensis</i>	<i>T. coriaceus</i>	Pink	Silent	
<b><u><i>C. shudikarensis</i></u></b>	3.1	2.4	2.3	0.8	143
<b><u><i>T. coriaceus</i></u></b>	0.0	3.8	0.3	0.2	73
<b><u><i>O. leprieurii</i></u></b>	0.0	1.7	0.0	0.0	20
<i>O. taurinus</i>	0.0	0.3	0.3	0.0	5
<i>C. cornuta</i>	0.0	0.2	0.2	0.0	2
<b><i>S. sp. 3</i></b>	0.0	0.2	0.0	0.0	1
<i>S. sp. 2</i>	0.1	0.1	0.0	0.0	2
<i>D. sp. 1</i>	0.0	0.0	0.0	0.1	1
<i>D. minutus</i>	0.1	0.1	0.0	0.2	6
<i>L. mystaceus</i>	0.0	0.0	0.0	0.3	5
<i>P. vaillanti</i>	0.1	0.0	0.0	0.1	3
<i>C. tomopterna</i>	0.2	0.2	0.1	0.0	8
<i>R. castaneotica</i>	0.1	0.1	0.0	0.0	2
<i>A. andreae</i>	0.0	0.0	0.1	0.0	1
Total	62	140	39	31	272

353

354

355 Table 2: Parameter estimates and 95% confidence intervals for best fit model predicting number  
 356 of individuals found on the traps as a function of playback stimuli in tropical explosive breeding  
 357 species. Parameter estimates are shown as differences with respect to the first category (Intercept)  
 358 in each variable (silent playback stimulus and species *Chiasmocleis shudikarensis*).

<b>Predictor</b>	<b>Estimate</b>	<b>Confidence intervals</b>	<b>z value</b>	<b>Pr(&gt; z )</b>
(Intercept)	-0.67	-1.64 0.30	-1.345	0.1785
<i>Osteocephalus leprieuri</i>	-2.54	-3.51 -1.57	-5.141	2.74E-07 ***
<i>Trachycephalus coriaceus</i>	-1.76	-2.53 -0.99	-4.483	7.35E-06 ***
Stimulus Pink noise	0.97	-0.01 1.96	1.940	0.0523
Stimulus <i>C. shudikarensis</i>	1.00	0.07 1.93	2.116	3.43E-02 *
Stimulus <i>T. coriaceus</i>	3.07	2.09 4.06	6.102	1.05E-09 ***

359  
 360  
 361  
 362

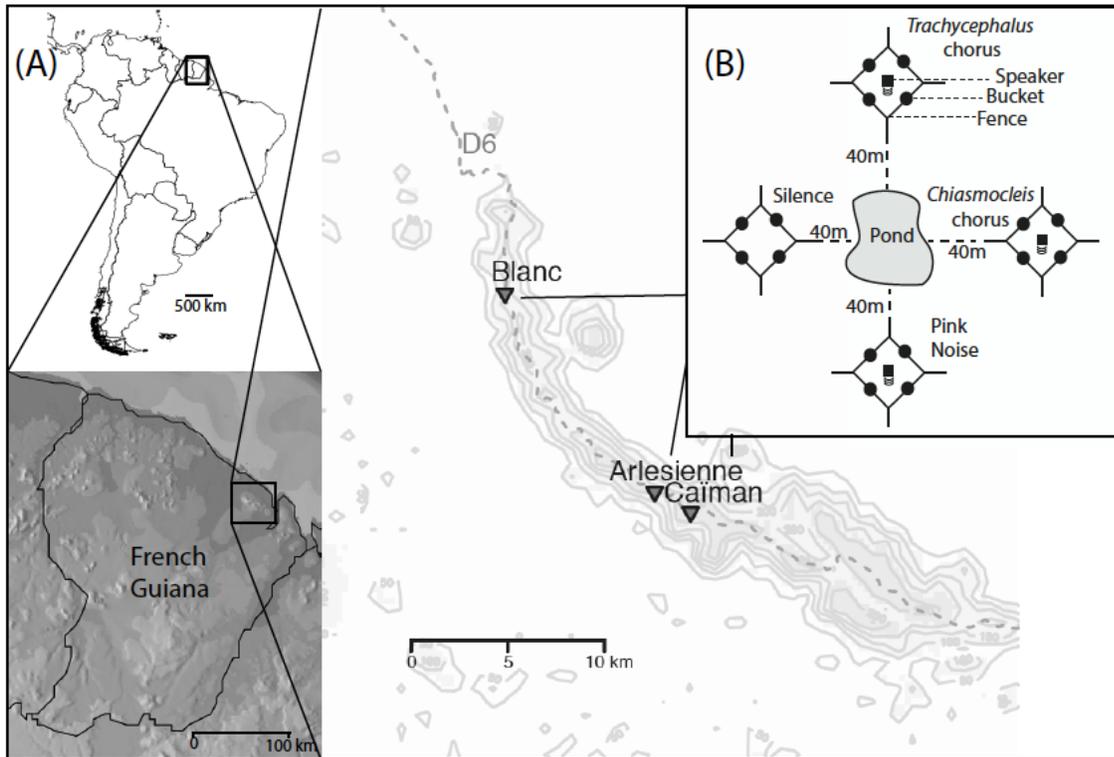


Figure 1

363

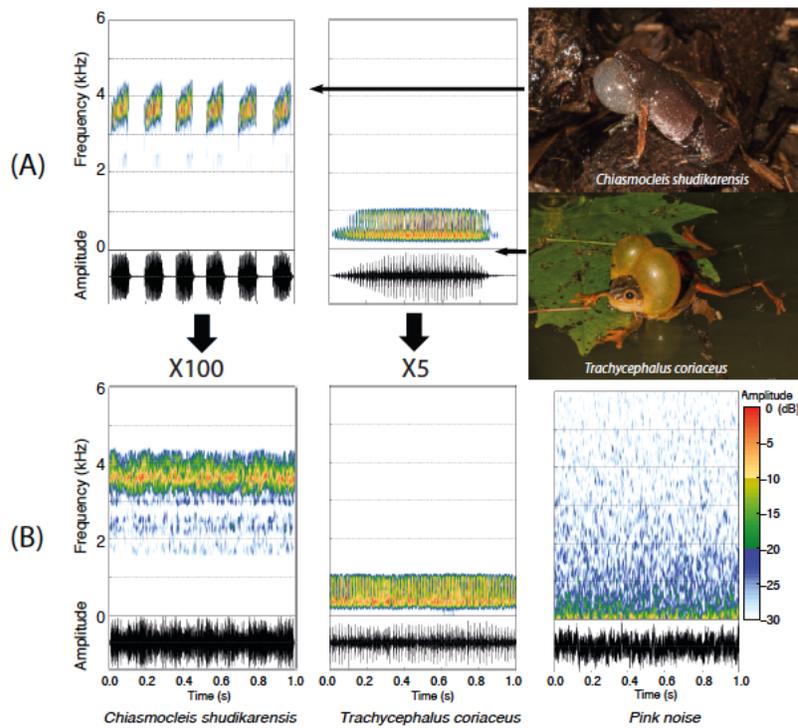
364 **Site location and experimental setup.** (A) Map of French Guiana and the Kaw Mountain with

365 the location of the three temporary ponds, the access road (D6 dotted grey line). (B) The diagram

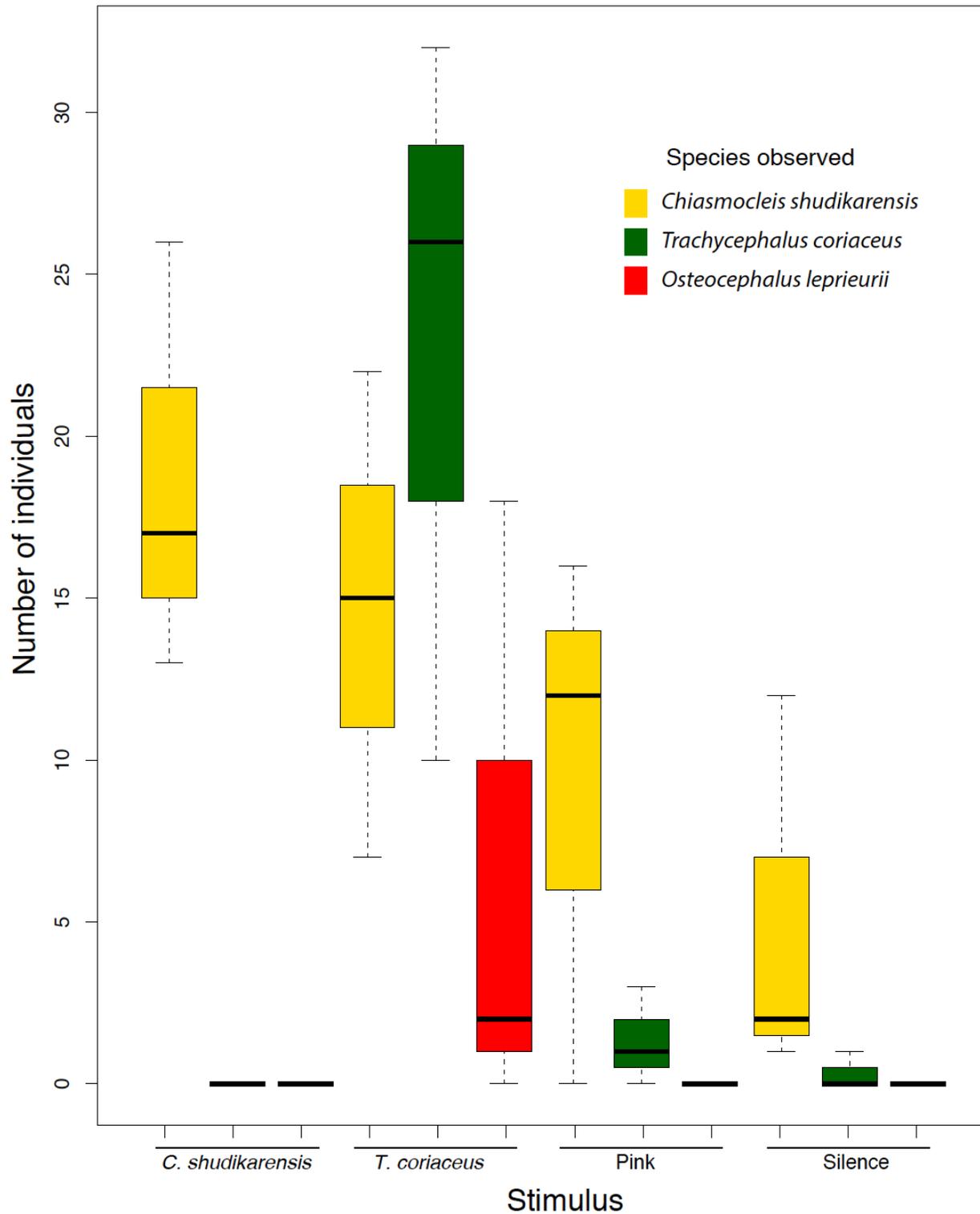
366 of the experimental setup deployed at each pond depicting the four positions where acoustic

367 stimuli were played back. Each loudspeaker was surrounded by diamond-shaped fence and pitfall

368 traps.



369  
 370 **Figure 2 Acoustic stimuli.** (A) One-second spectrograms and waveforms of the recordings used  
 371 to build the *C. shudikarensis* call and the *T. coriaceus* call signals after high-pass filtering. (B)  
 372 One-second spectrograms and waveforms of the generated stimuli mimicking choruses of *C.*  
 373 *shudikarensis* (~ 100 individuals) and *T. coriaceus* (~ 25 individuals) and the pink noise used in  
 374 the playback experiments. Short-term Fourier transform parameters: sampling frequency of 44.1  
 375 kHz, Hanning window of 500 samples with an overlap of 90 %, 30 dB dynamic range. Obtained  
 376 with Seewave R package (Sueur *et al.* 2008). Pictures show males of each species while calling.  
 377 Note the inflated vocal sacs. Pictures by Antoine Fouquet.



378  
 379 Figure 3 **Boxplot of the mean number of individuals** over the three ponds (summed for the 6  
 380 nights) of the most abundant species found with the four stimuli (*C. shudikarensis*, *T. coriaceus*,  
 381 pink noise and silent control). Note that *Osteocephalus leprieurii* is a species that does not breed  
 382 in the pond “Blanc”.

383

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405 Naturel” and the committee of the “Reserve Naturelle des Marais de Kaw-Roura” where the  
406 experiment took place. This study was permitted after careful consideration of its impacts. We  
407 also adhere to the “Guidelines for use of live amphibians and reptiles in field and laboratory

408 research” by the Herpetological Animal Care and Use Committee (HACC) of the American  
409 Society of Ichthyologists and Herpetologists. The study took place after the main breeding event  
410 of the study species therefore minimizing the lasting effect on the population. Our experiment  
411 attracted several species to the sound source during the playback, but it did not trigger breeding  
412 and the animals dispersed after the playback. Any potential disturbance to other fauna by the  
413 playback, the noise due to the generator powering the speakers, and the presence of the  
414 experimenters in the area lasted for three hours each night, was temporary and localized to small  
415 areas. The manipulation of animals was limited to very brief displacements of a few meters. The  
416 study required digging of holes (16 per pond, 4 stations of 4 traps) for pitfall traps but these were  
417 refilled at the end of the experiment.

418

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