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1 Acoustic orientation in the great crested newt (*Triturus cristatus*)

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23 Short title: heterospecific acoustic attraction in a newt

24 **Abstract.** We carried out laboratory experiments to determine whether orientation during  
25 migration in the great crested newt (*Triturus cristatus*) is influenced by acoustic  
26 information. Newts retrieved during the aquatic breeding seasons (adults), as well as during  
27 the terrestrial phase after breeding (adults and juveniles), were subjected to calls from  
28 sympatric (*Rana temporaria* and *Bufo bufo*) and allopatric (*Lithobates catesbeianus*)  
29 anurans. In addition to natural stimuli, we also used modified anuran calls (continuous  
30 sound with inter-note intervals removed), white noise with and without envelop, and a  
31 heterochthonous sound (pile driving). In a circular arena, adult newts retrieved both during  
32 their aquatic and terrestrial phase orientated towards the *B. bufo* stimulus, and migrated at  
33 random directions when exposed to the other calls; the lack of orientation towards the  
34 sympatric *R. temporaria* parallels a largely non-overlapping breeding season.  
35 Inexperienced juveniles did not orientate towards anuran calls, suggesting that phonotactic  
36 responses could be learned. Both aquatic as well as terrestrial adults significantly moved  
37 away from a white noise envelop. The results suggest different degrees of heterospecific  
38 call attraction across life stages, and provide evidence that unnatural sound might have an  
39 adverse effect on breeding migrations.

40

41 Keywords: Heterospecific attraction, acoustic orientation, homing, *Triturus cristatus*

42

## 43 **Introduction**

44 During migration, amphibians rely on a number of mechanisms for orientation (Adler, 1982;  
45 Phillips, 1998; Sinsch, 2006). Ferguson (1971) first proposed the redundant–multisensory system  
46 whereby amphibians integrate acoustic, magnetic, mechanical, olfactory and visual cues. The  
47 ranking of the sensory input obtained from these potential cues into a distinct hierarchy is  
48 species- as well as case-specific, and optimises the available information at any given time. In  
49 addition to external cues, more recent studies also accumulated evidence that amphibians rely on  
50 spatial memory, including the ability for cognitive flexibility (Crane and Mathis, 2011; Pašukonis  
51 et al., 2014; Pašukonis et al., 2016; Liu et al., 2016; Munteanu et al., 2016).

52 The idea that animals make orientation choices based on the position of conspecific  
53 individuals can be traced back many decades (e.g. Lack, 1948). In amphibians, conspecific  
54 attraction can alter habitat choice, and acoustic playbacks have recently been suggested as a  
55 conservation tool to improve the use of restored habitat (James et al., 2015; Pizzatto et al., 2016).  
56 The heterospecific attraction hypothesis (first described in birds: Mönkkönen *et al.*, 1990), on the  
57 other hand, refers to a scenario where migrant individuals use the presence of another species as a  
58 cue for profitable breeding sites, thereby preferentially approaching such habitat patches  
59 (Sebastian-Gonzalez *et al.*, 2010). Urodele amphibians lack tympanic middle ears (Smith, 1968),  
60 and rely on lateral body walls and lungs for sound reception (Hetherington, 2001; Capshaw &  
61 Soares, 2016; Crovo et al., 2016). Nevertheless, heterospecific acoustic attraction has been  
62 supported in adults of three species of pond-breeding European newts (*Triturus marmoratus*,  
63 *Lissotriton helveticus*, *L. vulgaris*), which in experimental arenas orientate towards calls of  
64 sympatric (but not allopatric) anurans (Diego-Rasilla and Luengo, 2004, 2007; Pupin et al.,  
65 2007). When switching from aquatic phases to life on land, urodeles undertake a range of  
66 morphological changes, for example developing a more tuberculated skin which becomes more

67 permeable to water (Toledo and Jared, 1993). However, while such changes have significant  
68 consequences to their acoustic sensory abilities (Christensen et al., 2015), it remains to be studied  
69 whether they are also reflected in differential acoustic orientation behaviour across aquatic and  
70 terrestrial life stages.

71 The great crested newt (*T. cristatus*) is the largest newt species in northern Europe (Jehle et  
72 al., 2011). Although *T. cristatus* often serves as an umbrella species for the conservation  
73 management of ponds and their surroundings, comparatively little is known about orientation  
74 during terrestrial migrations. While the ability to navigate in unfamiliar areas appears largely  
75 absent, close-range homing migrations appear to be largely based on olfactorial cues (Sinsch,  
76 2007; Hayward et al., 2000; Sinsch and Kirst, 2015). In the present paper, we focus on *T.*  
77 *cristatus* to extend previous studies on heterospecific attraction in newts to a range of different  
78 life stages (adults and juveniles). We distinguish individuals retrieved during the aquatic breeding  
79 season from newts captured terrestrially after the breeding season, and additionally consider  
80 juveniles who have never experienced a breeding season. We further test whether *T. cristatus*  
81 individuals phonotactically respond to modified anuran calls (continuous sound without notes), as  
82 well as non animal-borne cues (white noise and a heterochthonous anthropogenic sound).

83

## 84 **Materials and Methods**

85

### 86 *Study Site and Capture Methodology*

87 *Triturus cristatus* study individuals were retrieved from Rixton Clay Pits, Cheshire, England  
88 (National Grid Reference SJ 685 902) which support one of the largest known breeding  
89 population of *T. cristatus* in the United Kingdom. Newts during their aquatic phase were  
90 collected through dip netting on 31<sup>st</sup> May 2013 (18 males and 22 females). Newts during their

91 terrestrial phase after breeding were retrieved on 4<sup>th</sup> October 2013 through a hand search of  
92 potential refugia within 500 metres of the study ponds, yielding 10 males, 12 females and 12  
93 juveniles that metamorphosed earlier in the study year (as evidenced by their size and weight).  
94 All newts were transported to the laboratory where they were housed in individually labelled  
95 opaque plastic containers (170 mm radius, 40 mm high) with approximately 5 mm of water.  
96 Newts were not fed during captivity, and released at their place of capture after a maximum of 5  
97 days.

98

### 99 *Experimental Procedures*

100 The experimental procedure largely followed Diego-Rasilla and Luengo (2004; 2007) and Pupin  
101 *et al.* (2007). Newts were tested indoors on level arenas consisting of a plastic sheet (700 mm<sup>2</sup>  
102 and 3 mm thick), with a print of a compass at five degrees accuracy (600 mm in diameter)  
103 adhered to the underside (Figure 1). Wooden frames (750 mm<sup>2</sup> and 200 mm high) enclosed the  
104 arenas to prevent escape and to provide a barrier for external cues. One speaker (50 mm radius)  
105 was fixed to the outside of the frame so that sound could be directed through a circular hole  
106 towards the inside of the arena (Figure 1). This allowed the frame to alter the compass direction  
107 of each acoustic stimulus in four directions (0°, 90°, 180° and 270°) to factor out any consistent  
108 non-acoustic bias. To eliminate possible olfactory cues, the arena was thoroughly cleaned with a  
109 damp cloth and wiped dry using clean paper towels prior to each trial. The centre of the arena  
110 was then lightly sprayed with water to allow the directional response of each newt to be recorded  
111 by a moist trail on the arena floor. A release container (same opaque plastic container that newts  
112 were housed in) was placed in the centre of the arena, and manually lifted to release the newts.  
113 The experiments were undertaken in complete darkness, using a Mini Maglite® torch to prepare  
114 the arena for each trial.

115 A control (absence of acoustic stimuli) was used to factor out the presence of any external  
116 cues, and nine different acoustic stimuli were applied. To test for heterospecific attraction, two  
117 sympatric stimuli (the breeding calls of the anurans *Rana temporaria* and *Bufo bufo*, which are  
118 both present at the study site) and one allopatric stimulus (the breeding calls of the American  
119 bullfrog *Lithobates catesbeianus*) were broadcast to *T. cristatus* individuals; calls were taken  
120 from the species accounts on [amphibiaweb.org](http://amphibiaweb.org). To test which properties of acoustic information  
121 promote phonotaxis, these playbacks were also modified to constant sound (i.e. the frequency and  
122 amplitude were maintained but the silence between calls was removed). In addition to anuran  
123 stimuli, white noise was broadcast to determine whether acoustic signals generally stimulate a  
124 response, and a white noise envelope was produced to mimic the temporal pattern of anuran calls  
125 (0.6 s note duration with 0.6 s note interval). Finally, a pile driving recording  
126 (<http://freesound.org/people/LG/sounds/91762/>) was chosen to determine whether a  
127 heterochthonous sound such as stemming from human activities elicits phonotaxis. Stimuli were  
128 modified using the software Audacity. All playbacks were reset at the beginning of each trial, and  
129 broadcast in their entirety on a continuous loop using an iPod Classic<sup>®</sup>. The sound pressure level  
130 of the acoustic stimuli, measured from the centre of the arena with a Digital Sound Level Meter  
131 (Maplin sound level meter N33GJ), was calibrated to 68 dB, corresponding to the sound pressure  
132 level generated by a typical anuran approximately 10-12 m from a breeding pond (following  
133 Diego-Rasilla and Luengo, 2004).

134 Prior to release, newts were kept in complete darkness and acoustically isolated from the  
135 test arena. Individuals were selected at random and left undisturbed under the release container  
136 for 1 minute to overcome the effects of handling. Movements were recorded after 5 minutes to an  
137 accuracy of 5°, and direction was determined through the first point at which the moist trail  
138 trespassed the compass border (300 mm from the release point). Successfully trialed newts were

139 returned to their container, and stored separately from un-trialed newts. Individuals that did not  
140 reach the orientation criterion within the set time interval were returned to their container and  
141 stored with the un-trialed newts ready for random selection.

142 The acoustic stimuli and the compass direction at which it was broadcast were randomly  
143 defined for each trial. Data from the four directions were combined for each data set by rotating  
144 the bearings so that the acoustic stimuli compass directions coincided at 0° (i.e., 90, 180 and 270  
145 was subtracted from the actual headings of newts tested with the acoustic stimuli broadcast from  
146 90°, 180°, and 270°, respectively; Diego-Rasilla and Luengo, 2004). Data were analyzed using  
147 standard circular statistics (Batschelet, 1981; Fisher, 1995) and the software PAST (Hammer *et*  
148 *al.*, 2001). Mean vectors ( $\mu$ ) were calculated by vector addition. The *V* test, a modified Rayleigh  
149 test, was used to test for significant movements in relation to the direction of the stimuli. We  
150 considered both positive and negative phonotaxis by testing for an association with 0° and 180°  
151 from the stimulus, respectively; *P* value intervals were derived from the table provided in  
152 Batschelet (1981). The Mardia-Watson-Wheeler test was performed to assess whether pairwise  
153 samples differed significantly from each other (Batschelet, 1981; Zar, 1984). Males and females  
154 were pooled for analyses as no differences in orientation between the sexes were found (detailed  
155 data not shown).

156

## 157 **Results**

158

159 A total of 820 trials based on 82 study individuals were undertaken; 400 trials by newts captured  
160 during the aquatic breeding phase, and 420 trials by newts captured during the terrestrial phase.  
161 The majority of trials (725; 88.4%) were successful during the first attempt, and 9.5% of trials  
162 were successful during the second attempt; a further 1.6% and 0.5% of newts had to be trialled



163 three and four times, respectively. Eighty-two percent of the re-trials are based on initial trials  
164 which were conducted in the absence of acoustic stimuli (control), supporting that newts are more  
165 reluctant to orientate in the absence of an acoustic cue.

166 The data obtained for the control (no stimulus) and the three unmodified anuran call  
167 stimuli are shown in Figures 2-4, a-d. All experimental groups orientated randomly under the  
168 control situation in the absence of an acoustic stimulus ( $P > 0.05$  in all cases); significance was  
169 tested with the home direction set to the mean vector bearing as well as all four cardinal points  
170 ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$  and  $270^\circ$ ), demonstrating that the experimental setup was free from directional  
171 bias. Aquatic and terrestrial adults significantly orientated towards calls of *B. bufo* (aquatic:  $V$  test  
172 with expected direction =  $0^\circ$ ,  $r = 0.29$ ,  $n = 40$ ,  $U = 2.59$ ,  $P < 0.005$ , Figure 2b; terrestrial:  $r = 0.40$ ,  
173  $n = 32$ ,  $U = 2.67$ ,  $P < 0.005$ , Figure 3b), with a directional responses which did not differ  
174 significantly from each other (Mardia-Watson-Wheeler test:  $P_{\text{same}} = 0.997$ ). Juveniles, on the  
175 other hand, showed no phonotactic reaction towards the *B. bufo* call ( $r = 0.23$ ,  $n = 10$ ,  $U = 0.43$ ,  $P$   
176  $> 0.05$ , Figure 4b). When exposed to the calls of the sympatric *R. temporaria*, neither terrestrial  
177 nor aquatic adults migrated significantly towards the stimulus (aquatic:  $r = 0.14$ ,  $n = 43$ ,  $U = -$   
178  $0.88$ ,  $P > 0.05$ , terrestrial:  $r = 0.23$ ,  $n = 22$ ,  $U = -1.54$ ,  $P > 0.05$ ; Figures 2c and 3c). The Mardia-  
179 Watson-Wheeler test confirmed that the aquatic and terrestrial adults orientated similarly ( $P_{\text{same}} =$   
180  $0.877$ ). Again, juveniles showed no reaction to the stimulus ( $r = 0.10$ ,  $n = 10$ ,  $U = 0.43$ ,  $P > 0.05$ ,  
181 Figure 4c). *Litobathes catesbeianus* calls elicited a similar response to that of *R. temporaria*,  
182 again without significant orientation towards the stimulus (aquatic:  $r = 0.13$ ,  $n = 43$ ,  $U = 1.05$ ,  $P$   
183  $> 0.05$ , terrestrial:  $r = 0.10$ ,  $n = 22$ ,  $U = -0.23$ ,  $P < 0.05$ , Figures 2d and 3d), and a directional  
184 responses which is indiscernible between aquatic and terrestrial newts (Mardia-Watson-Wheeler  
185 test  $P_{\text{same}} = 0.729$ ). *Lithobates catesbeianus* also did not solicit a significant response from  
186 juveniles ( $r = 0.16$ ,  $n = 12$ ,  $U = -0.79$ ,  $P < 0.05$ , Figure 4d). For all experiments, tests for

187 negative phonotaxis revealed no significant results ( $P > 0.05$  in all cases, detailed data not  
188 shown).

189 The results for modified and non animal-born cues are summarised in Table 1. Adult *T.*  
190 *cristatus* from both life stages significantly moved away from interrupted white noise, and the  
191 Mardia-Watson-Wheeler test illustrated that the directional response of aquatic and terrestrial  
192 adults were indiscernible ( $P_{\text{same}} = 0.169$ ). All other stimuli did not result in significant positive or  
193 negative phonotaxis towards the tested stimuli.

194

## 195 **Discussion**

196 As has previously been shown for other European newt species (the congeneric *T. marmoratus*  
197 and two *Lissotriton* species, Diego-Rasilla and Luengo, 2004, 2007; Pupin *et al.*, 2007), this  
198 study confirms the use of heterospecific calls for *T. cristatus*. Moreover, this study  
199 shows for the first time that newts at different life stages respond differentially to acoustic cues.  
200 The control tests satisfied the absence of non-acoustic bias within the test arena, and that the vast  
201 majority of the re-trials were required for control situations (silence) suggests that individuals  
202 indeed made orientation decisions based on acoustic stimuli. However, it is important to bear in  
203 mind that our experimental arenas represent an unnatural situation, and that the behavioral  
204 reactions may not be representative of field situations where a multitude of cues are available  
205 (Sinsch, 2006). Ideally, all stimuli would have been tested from all directions; however, the  
206 nature and biology of the species and limited timeframe permitted to keep the newts in captivity  
207 (specified as part of the license) prevented this approach. Instead, newts were tested so that the  
208 pooled data sets included roughly equal numbers of bearings with the acoustic stimuli broadcast  
209 from the four directions. The methodology used was specifically chosen to draw direct  
210 comparisons with previous studies, and given the time constraints attributed to protected species

211 offered the best solution to randomization and unbiased trials. Anuran calls are highly  
212 stereotyped and species-specific in their broad spectral and temporal properties (see Wells, 2007).  
213 Standardizing the stimuli of different species to the same call rates would therefore lead to  
214 unrepresentative comparisons, and we restricted ourselves to a standardized SPL at stimuli whose  
215 temporal properties are typical for each species.

216 Heterospecific attraction of *T. cristatus* towards *B. bufo* but not *R. temporaria* supports  
217 results previously reported for other newt species. Diego-Rasilla and Luengo (2007, with *L.*  
218 *helveticus*) attributed this observation to a largely non-overlapping breeding season which might  
219 lead to calls which are unfamiliar for orientation (at our study site, *R. temporaria* breeds  
220 approximately 4 weeks before the peak immigration of *T. cristatus* and *B. bufo*, unpublished  
221 observations). It however should be acknowledged that the experiments with terrestrial newts  
222 were conducted during a time of the year when anurans do not call naturally, and still elicited a  
223 response to *B. bufo*. The lack of attraction of adults to the unfamiliar *L. catesbeianus* further  
224 confirms that urodeles are capable of discriminating between calls from different anurans (Diego-  
225 Rasilla and Luengo, 2007). It however remains to be studied whether our phonotaxis experiments  
226 were influenced by ignoring phylogeographic differences in fine-scale properties of calls (e.g.  
227 Wycherley et al., 2002).

228 Natural selection should favour amphibians which are capable of efficiently using a range  
229 of migration cues, for example to reduce the risk of predation during orientation (Bonachea and  
230 Ryan, 2011). Diego-Rasilla and Luengo (2004) demonstrate that heterospecific attraction only  
231 takes place towards species which are naturally present at a given site, suggesting that this  
232 behaviour could be altered through learning. This is supported by our data from juvenile  
233 individuals, which were not attracted to any of the three anuran calls (at a however low small  
234 sample size of 10 individuals). Juveniles have not yet experienced a breeding season and are

235 therefore unfamiliar to such potential acoustic migration cues, although they for example follow  
236 scent trails of conspecific adults (Hayward et al., 2000). Learning has been previously  
237 demonstrated for *T. cristatus* (e.g. Hershkowitz and Samuel, 1973), and other urodeles learn to  
238 use landmarks for finding food and avoid dangerous habitat types based on predatory olfactory  
239 cues (Crane and Mathis, 2011). It is furthermore in line with the observation that *T. cristatus* has  
240 the ability to orientate towards breeding ponds within a range of familiarity (Sinsch, 2007; Sinsch  
241 and Kirst, 2015), and that individual *T. cristatus* return to specific terrestrial refuge areas after  
242 displacement into the breeding pond (Jehle, 2000).

243         Most studies regarding urodele orientation suggest that magnetic (Phillips, 1986; Fischer  
244 et al., 2001; Diego-Rasilla et al., 2008), celestial (Landreth and Ferguson, 1967; Diego-Rasilla  
245 and Luengo, 2002), and olfactorial (Joly and Miaud, 1993; Sinsch and Kirst, 2015) cues are  
246 amongst the primary sources for directional choices. However, individuals whose breeding sites  
247 have disappeared or have become displaced (translocation is a common management practice for  
248 *T. cristatus* for example in the United Kingdom, Jehle et al., 2011) may increasingly also rely on  
249 acoustic cues. That newts were significantly attracted to heterospecific calls could in the future be  
250 used to facilitate a more efficient colonization of newly created habitat, as has already been  
251 suggested for anurans based on conspecific calls (James et al., 2015). That individual *T. cristatus*  
252 moved away from the white noise envelope further suggests that newts might be affected by  
253 monotonous anthropogenic noise. This is a particular concern given that e.g. mineral extraction  
254 sites represent important habitats in many parts of the *T. cristatus* range (Jehle et al., 2011),  
255 although the more heterochthonous stimulus typical for e.g. construction sites (pile driving) had  
256 no significant effect on orientation.

257

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261

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263

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346



347 Table 1: Summary of responses of adult (aquatic and terrestrial) and juvenile great crested newts  
 348 (*Triturus cristatus*) to modified acoustic stimuli. Values represent the *u* test statistic for  
 349 significant relationships between migrations and the direction of stimuli based on *V*-tests;  
 350 positive and negative values denote positive and negative phonotaxis, respectively. \*:  $p < 0.05$ .  
 351

Stimulus	Adults (aquatic) <i>n</i> = 40	Adults (terrestrial) <i>n</i> = 32	Juveniles <i>n</i> = 10
White noise	1.45	-0.96	-1.60
White noise (interrupted)	-1.99*	-1.68*	-1.57
<i>Bufo bufo</i> (continuous)	-0.91	1.28	1.10
<i>Rana temporaria</i> (continuous)	-0.91	-0.20	1.10
<i>Lithobates catesbeianus</i> (continuous)	-1.24	0.16	0.06
Pile driving	-0.80	0.55	0.41

352  
 353  
 354  
 355

356 Figure legends:

357

358 Figure 1: Arena design used during the experiments.

359

360 Figure 2. Circular diagram representing the orientation responses of adult *Triturus cristatus*  
361 captured during the aquatic phase to a) a control stimulus (silence); b) *Bufo bufo*, c) *Rana*  
362 *temporaria*, and d) the allopatric stimulus *Lithobates catesbeianus*.

363

364 Figure 3. Circular diagram representing the orientation responses of adult *Triturus cristatus*  
365 captured during the terrestrial phase to a) a control stimulus (silence), b) *Bufo bufo*, c) *Rana*  
366 *temporaria*, and d) the allopatric stimulus *Lithobates catesbeianus*.

367

368 Figure 4. Circular diagram representing the orientation responses of juvenile *Triturus cristatus* to  
369 a) a control stimulus (silence), b) *Bufo bufo*, c) *Rana temporaria*, and d) the allopatric stimulus  
370 *Lithobates catesbeianus*.

371

Figure 1.

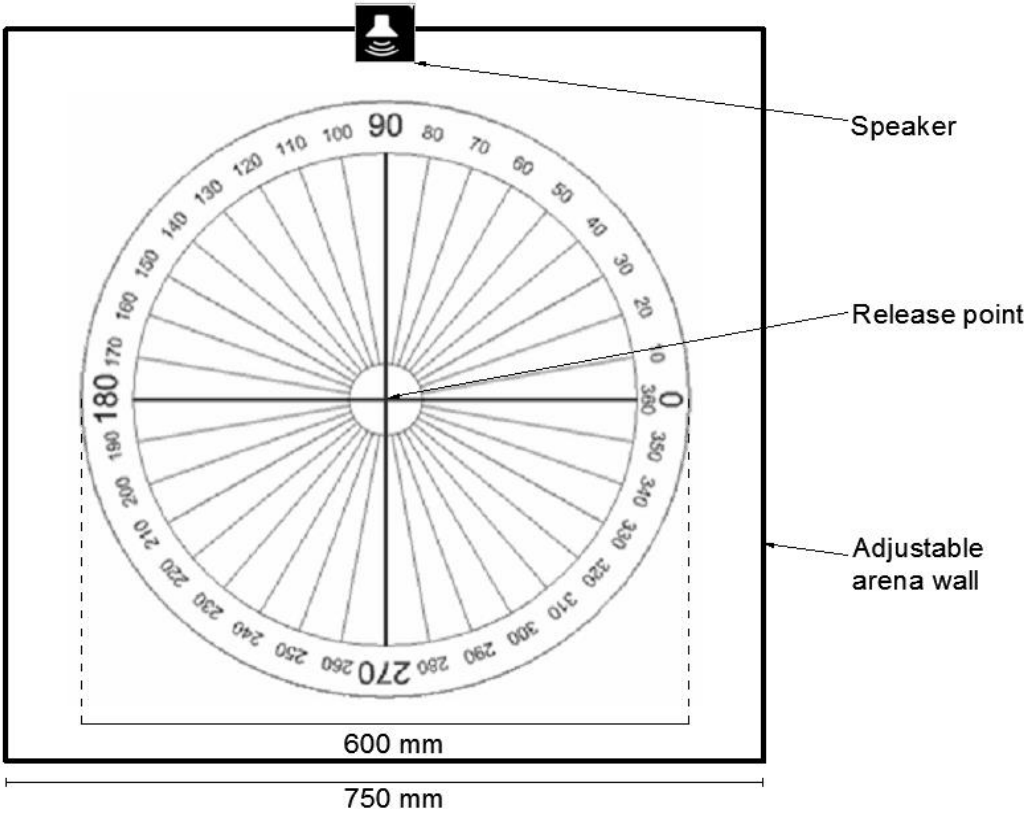


Figure 2:

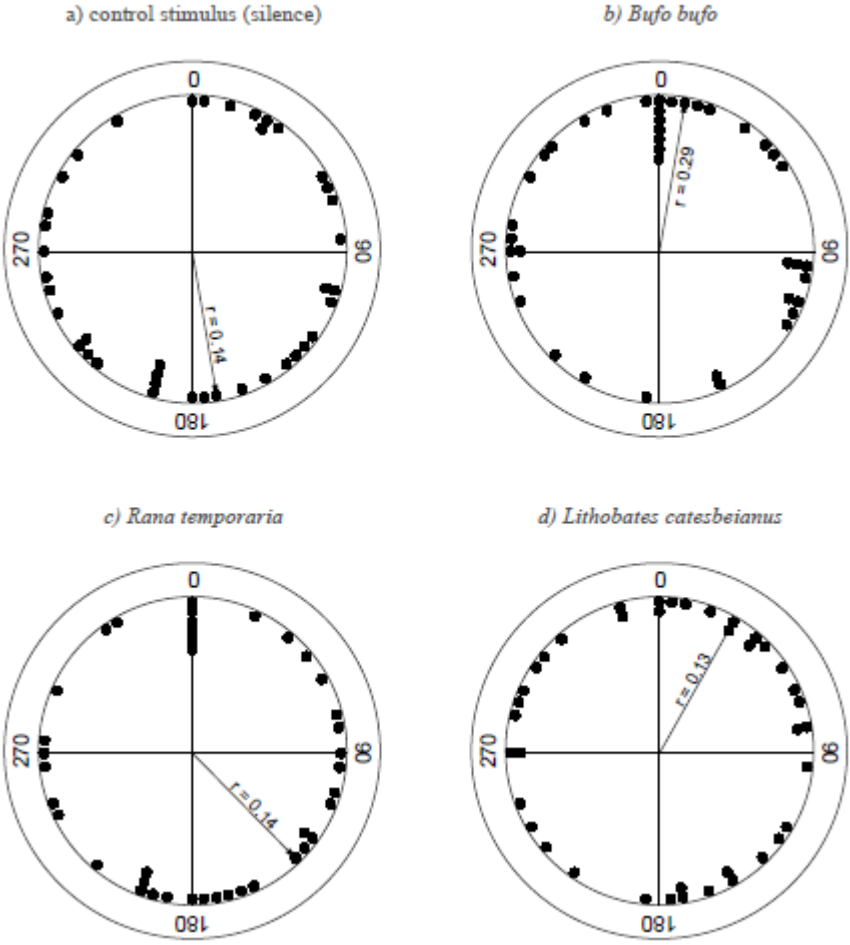


Figure 3:

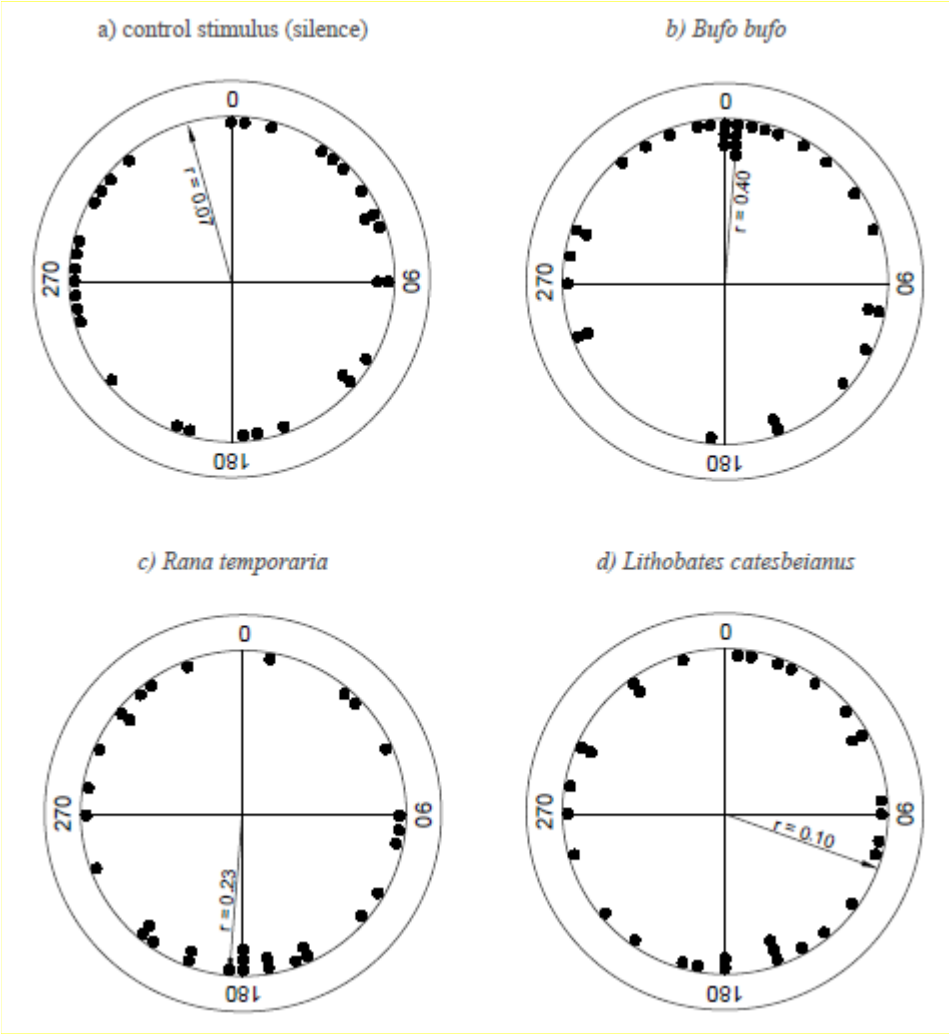


Figure 4:

