

Effects of simulated call distance on behaviour in *Hyla arborea* and *Pelobates fuscus*

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Accepted August 12, 2026

Published online September 30, 2026

Issue online September 30, 2026

Short communication

BEŁCIK M., WOŹNIAK B., WOŹNIAK P., SKÓRKA P. 2026. Effects of simulated call distance on behaviour in *Hyla arborea* and *Pelobates fuscus*. Folia Biologica (Kraków) 74: 59-67.

Acoustic communication plays a central role in the reproductive and social behaviour of anurans, influencing not only mate attraction and male–male interactions but also the spatial structure of breeding assemblages. Because sound propagation is constrained by environmental factors, the effective communication range determines how individuals perceive one another across the landscape. While the acoustic properties of frog calls have been studied extensively, less is known about how the receivers behaviourally respond to calls simulating different source distances. We examined how the simulated call distance and weather conditions affect behavioural responses in two ecologically and acoustically contrasting amphibians: the European tree frog (*Hyla arborea*); and the Common spadefoot (*Pelobates fuscus*). Both species were tested under semi-natural conditions using playback experiments in which conspecific advertisement calls were broadcast at levels corresponding to various source distances. Individual positions within an arena were recorded over time as angular absolute deviations from the loudspeaker sector, with low deviations indicating attraction while large deviations indicated avoidance behaviours. The behavioural data was analysed using generalised linear mixed models with Gamma and binomial error structures. For *H. arborea*, the angular deviations from the loudspeaker significantly increased with the temperature but not with the simulated distance, time nor the humidity. For *P. fuscus*, no significant relationship between the position of an individual relative to the playback source was detected, nor with the distance, time, temperature and humidity, which is consistent with the limited importance of acoustic competition in this fossorial species. We observed the immobility of several individuals of *P. fuscus*, which stayed in the centre of the experimental arena. The probability of the occurrence of this behaviour increased with the air humidity. These findings, contrary to our expectations, suggest that a frog's movement behaviour depends on environmental conditions rather than on the social context and spatial scale.

Key words: acoustic communication, playback experiment, distance perception, behavioural response, spatial ecology.

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Acoustic communication plays a key role in the social and reproductive behaviour of anurans. Male advertisement calls attract females and mediate male–male interactions, influencing spacing, territoriality and aggregation patterns (Gerhardt & Huber 2002). These signals may also shape the habitat usage, as their distribution and intensity affect how in-

dividuals occupy breeding sites (Bee 2002; Bosch & Márquez 2001). Because sound transmission is constrained by environmental factors such as the vegetation, humidity and temperature, the effective range of calls can influence how individuals perceive one another and how breeding populations are spatially structured (Wells 2007).



Acoustic signals degrade and attenuate with distance depending on the environmental conditions (Kroodsma & Miller 1982; Morton 1975), limiting the communication range and affecting the signal detectability and localisation. Anurans use cues such as amplitude and signal degradation to estimate the distance of calling conspecifics (Bee *et al.* 2000; Römer 1998). This ability is ecologically important, influencing the anurans' mate choice, territorial behaviour and spatial organisation. However, relatively little is known about the behavioural responses to calls simulating different distances, especially under natural or semi-natural conditions.

To address this, we examined two species differing in their ecology and acoustic behaviour: the European tree frog (*Hyla arborea*, Linnaeus 1758); and the Common spadefoot (*Pelobates fuscus*, Laurenti 1768). *H. arborea* is an arboreal species that forms large breeding choruses, with loud calls audible over long distances; whereas *P. fuscus* is fossorial, calling less frequently and producing quieter signals detectable only at close range (Andreone & Piazza 1990; Friedl & Klump 2002; Juszczuk 1974; Wells 2007). These differences make them suitable for comparing their responses to signals simulating varying distances.

The aim of this study was to examine whether the behavioural responses to conspecific advertisement calls vary with the simulated source distance. Using playback experiments, we tested the reactions to calls representing different apparent distances from the source and compared responses between the two species with contrasting acoustic characteristics. We compared the patterns of response to simulated call distances in two species differing in their acoustic ecology. Understanding such distance-dependent responses may help to explain how acoustic communication influences the spatial organisation and habitat usage in anurans.

Methods

Playback preparation

To obtain calls for the playback, vocalisations of 4 individuals of *H. arborea* and 10 individuals of *P. fuscus* were recorded from animals encountered in the study area (not captured). The recordings were made using a Tascam DR-05 recorder and a Sennheiser SM-67 microphone with a K6 module and windscreen. For each recording, the source distance and gain settings were noted. All the recordings were processed, and the equipment was calibrated. Playback stimuli were prepared as species-specific composite recordings consisting of calls from multiple recorded individuals. The acoustic parameters for these recordings are described in Table 1. The frequency response and sensitivity of the recording chain were determined using an FFT analysis of white noise under anechoic conditions, allowing for the derivation of an equalisation curve. The playback system was then evaluated by measuring the SPL for a 1 kHz tone at maximum volume, enabling a distortion assessment and calibration. The 1 kHz tone was chosen due to the relatively flat system response and consistency with the SPL meter calibration.

The frequency response of the playback chain was further measured (on- and off-axis) using a Behringer ECM-9000 microphone, and an additional correction curve was derived. The calibration accuracy was verified with a control white-noise recording; after applying corrections, a flat response (± 1.5 dB, 200 Hz–10 kHz) was achieved, which was sufficient for the analysed signals. Using this data, the SPL values were calculated for each recording and normalised to a 1 m distance assuming free-field propagation (6 dB decrease per doubling of distance). These values were used to determine the target playback levels. The recordings were converted

Table 1
Acoustic parameters of the recordings used in the playbacks

Species	<i>Hyla arborea</i>	<i>Pelobates fuscus</i>
No. recordings	4	10
No. calls measured	87	1211
Dominant frequency (Hz), mean $\pm$ SD	2043 $\pm$ 131	721 $\pm$ 247
Dominant frequency range (Hz)	1770–2389	250–1466
Call duration (ms), mean $\pm$ SD	90.8 $\pm$ 20.8	137.7 $\pm$ 86.4
Call duration range (ms)	64.9–175.4	69.7–851.1
Call rate (calls/min), mean $\pm$ SD across recordings	275.1 $\pm$ 150.8	24.7 $\pm$ 18.6
Call rate range (calls/min)	66.2–412.8	5.2–60.6

to 32-bit float, then corrected and exported as WAV (16-bit, mono). All of the processing was performed in Adobe Audition 3.01.

During the final setup, the loudspeaker distance was increased to 4 m, requiring a +12 dB level adjustment. This reduced the loudspeaker self-noise and minimised the effect of variability in the frogs' distance from the source.

The final playback setup was to simulate the following distances: 50 m, 100 m and 200 m for *H. arborea*; and 5 m, 10 m and 40 m for *P. fuscus*.

Capturing amphibians for the experiment

Prior to the experiment, 37 male European tree frogs (*H. arborea*) were captured using dip nets (we were unable to capture any females at the time). Moreover, 51 Common spadefoots (*P. fuscus*; 45 females and 6 males) were captured. Differences in the sex ratios between the species resulted from the sampling methods. All *H. arborea* individuals were collected in the field by locating calling males, whereas all *P. fuscus* individuals were collected at a single site (an abandoned swimming pool). A permit for handling amphibians was obtained from the Regional Directorate for Environmental Protection in Lublin (Permit No. WPN.6401.39.2019.KC). No ethical committee approval was required, as no invasive procedures were performed.

All of the individuals were handled with latex gloves to minimise contamination and stress, and the disturbance was kept to a minimum. Each animal was placed in a separate ventilated plastic container with a small amount of water from the capture site in order to maintain humidity. The *H. arborea* males were captured at the onset of their evening vocal activity, tested shortly afterward, and were released the same night or early the next morning. The *P. fuscus* individuals were kept in larger containers filled with moist moss, allowing for natural burrowing.

The containers were kept in a separate dark room, with minimal disturbance limited to maintaining the appropriate conditions (e.g. moisture). The *P. fuscus* individuals were not fed during captivity. After each session, all the individuals were released at their capture site, and no *P. fuscus* was held for more than three days. The distance between the capture and test sites ranged from 3 to 10 km.

Experimental design

The experiment was conducted between 19 May and 10 June 2019, corresponding to the peak breeding activity of both species (Juszczyk 1974; Wells 2007). The trials began after dusk (after 9 pm CET)

and continued until 3 am CET, matching the natural peak of the frogs' vocal activity. For *H. arborea*, the mean temperature and humidity during the experiment was $16.2^{\circ}\text{C} \pm 2.66$ SD (range: 12.9–21.4) and $89.0\% \pm 8.26$ SD (range: 72.0–98.0), respectively. For *P. fuscus*, the mean temperature and humidity during the experiment was $14.9^{\circ}\text{C} \pm 1.81$ SD (range: 13.0–18.6) and $81.7\% \pm 8.14$ (range: 75.0–97.0), respectively.

The experiment was carried out in an arena (Fig. 1), 1.5 m in diameter with an octagonal base divided into eight numbered sectors (1–8). The arena was placed on a lawn with low anthropogenic and natural background noise and no artificial light. Its sides were made of 1 m high polyester mesh. An infrared camera mounted above the arena recorded each trial. At a distance of 4 m from the arena wall, a JAM HX-P710 loudspeaker (set to maximum volume), paired with a Philips GoGear Azure SA5AZU08KF, was used for the playback. The loudspeaker was aligned with one of the sectors, and its position was randomised between trials. Five loudspeaker–player sets were used and were randomised, with an inter-unit variation below 1 dB, ensuring sufficient repeatability.

At the start of each trial, an individual was placed in the centre of the arena and covered with a small metal cage (Fig. 1). The recording began at this point, and the individuals remained under the cage for three minutes to acclimate. The cage was then lifted remotely, and the playback of *H. arborea* or *P. fuscus* calls was initiated, depending on the species being tested. The position of each individual was recorded at one-minute intervals, and the air temperature and the humidity were measured. The playback type was randomised across the trials, and each trial lasted five minutes. Each individual

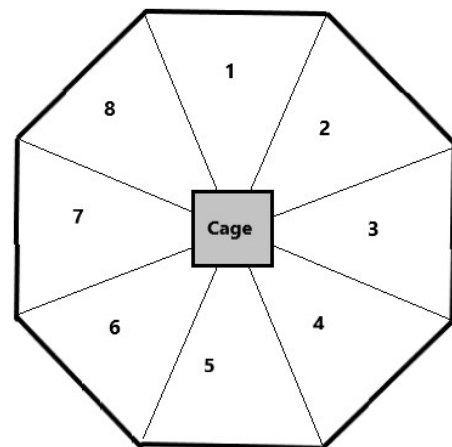


Fig. 1. Experimental arena used in the playback trials. The octagonal arena (1.5 m in diameter) was divided into eight equal sectors (1–8) with a central cage used for the initial acclimation of each individual.

was tested only once, and was submitted to a single species-specific composite playback stimulus (with three versions of this stimulus generated to simulate different source distances). Thus, the individuals of a given species were exposed to the same conspecific playback stimulus, differing only in the amplitude level corresponding to the assigned simulated distance treatment.

The data obtained from the experiment and used in the analyses are provided in Supplementary Materials 1 (SM.01.). All analyses were conducted in R (R Core Team 2021) using the tidyverse (Wickham *et al.* 2019), circular (Agostinelli & Lund 2025) and glmmTMB (Brooks *et al.* 2017) packages. Time-stamped behavioural observations (1-5 min) were reshaped into a long format (one row per individual $\times$ time). The position of the sector with each individual was converted into the angular deviation relative to the position of the loudspeaker, with values of 0°, 45°, 90°, 135° and 180°. Therefore, the individuals which moved towards playback source had a value of 0° at a given time, while individuals that strongly avoided the playback source were in the opposite sector (180°). This was our major response variable of interest called *Deviation*. In the case of *P. fuscus*, we also analysed another response variable called *Immobility* – whether the individual remained in the centre of the arena all the time (coded as 1) or moved to another sector of the arena (coded as 0). At the beginning, we used the Watson circular uniformity test to check if the distribution of frogs in the sectors deviated from a random distribution around the centre of the arena. For each species and the response variable *Deviation*, generalised linear mixed models with a Gamma distribution and log link function were used (Beck *et al.* 2017). We added a small value (0.5) to this variable as the model assumed non-zero data. In the case of *P. fuscus*, only the individuals that were mobile (moved outside the central point of the experimental arena) were used in this analysis.

For the response variable *Immobility*, a generalised linear mixed model with a binomial error distribution and complementary log–log link was fitted. The complementary log–log link was chosen over the logit link due to its asymmetric transformation, making it more suitable for rare-event binary data (Zuur *et al.* 2009). In each model, the fixed effect included the simulated broadcast distance (categorical variable) and the following covariates: observation time, temperature (°C) and humidity (%). These covariates were weakly or moderately correlated among each other (Table 2). Individual identity nested in the loudspeaker identity was included as a random factor to account for the repeated measurements of the behaviour of one individual. The R script used to perform the statistical analyses is provided in Supplementary Materials 2 (SM.02).

Results

The distribution of *H. arborea* individuals in the arena was non-random (Watson test, $U = 3.524$, $p = 0.01$, Fig. 2) indicating that some factors influenced their movements. The generalised linear mixed models indicated that the mean absolute angular deviation increased significantly with an increasing temperature (Table 3, Fig. 3), while the effect of the remaining variables was not significant. The random effect of the individual identity accounted for a moderate variation (variance = 1.26, SD = 1.125), but the variation among speakers was close to zero (variance < 0.001, SD < 0.001).

The distribution of *P. fuscus* individuals in the arena was also non-random (Watson test, $U = 5.934$, $p = 0.001$, Fig. 2). However, the generalised linear mixed models indicated that none of the variables was correlated with an absolute angular deviation (Table 3). The random effect of the individual identity had a high value (variance = 2.10, SD = 1.450), while

Table 2

Matrix of correlation coefficients among covariates used in the statistical analyses for *Hyla arborea* and *Pelobates fuscus*. Significance: *** $p < 0.001$

<i>Hyla arborea</i>			
Variables	Time	Temperature	Humidity
Time	1	0.13	0.49 ***
Temperature	0.13	1	-0.12
Humidity	0.49***	-0.12	1
<i>Pelobates fuscus</i>			
Variables	Time	Temperature	Humidity
Time	1	-0.11	0.02
Temperature	-0.11	1	-0.54***
Humidity	0.02	-0.54***	1

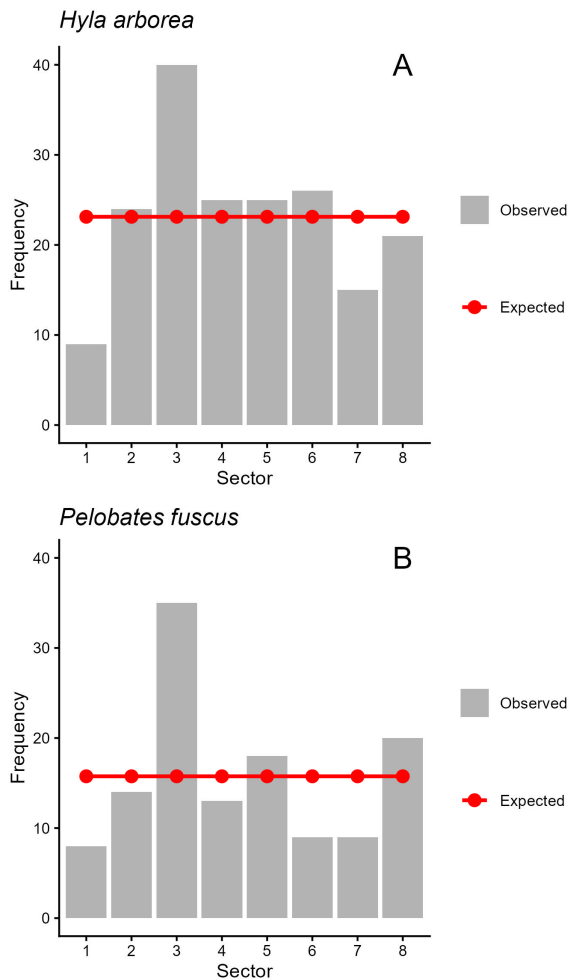


Fig. 2. Distribution of individuals of: A – *Hyla arborea* and B – *Pelobates fuscus* in different sectors of the experimental arena. The red horizontal line and dots indicate the expected numbers of individuals in sectors, assuming their random distribution.

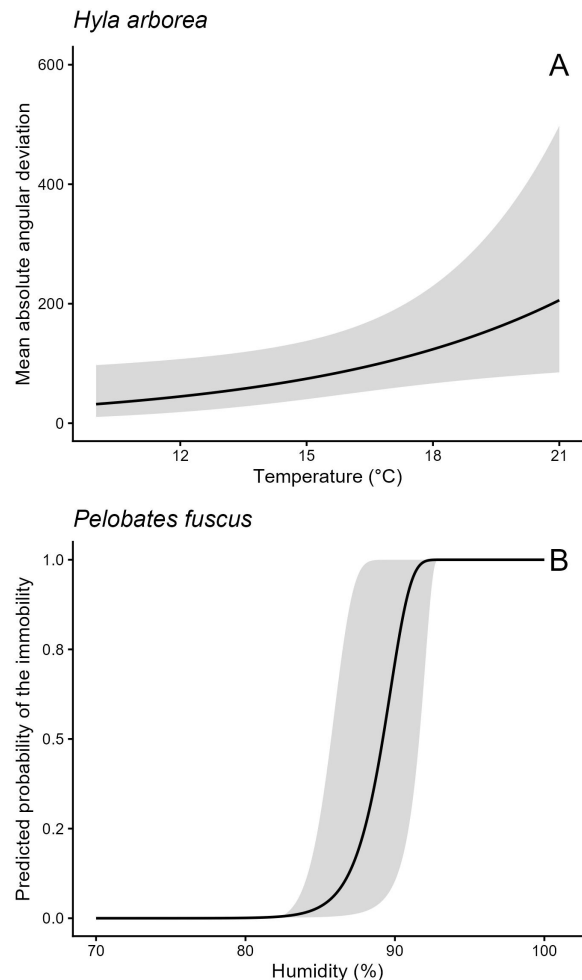


Fig. 3. Predicted effects of: (A) temperature on the angular deviations of *Hyla arborea*; and (B) humidity on the immobility of *Pelobates fuscus*. Solid lines represent model predictions; shaded areas denote 95% confidence intervals.

the speaker identity very low (variance < 0.001, SD < 0.0001). The immobility of *P. fuscus* was positively correlated with the humidity, but not with the other variables (Table 3, Fig. 3). The random factor of the individual identity had a moderate variance equalling 2.1 (SD = 1.45) and the loudspeaker identity had a negligible variance (variation < 0.001, SD = 0.0002).

Discussion

In this study, we tested whether two anuran species with contrasting acoustic ecologies would respond differently to conspecific calls simulating different source distances. Contrary to our expectations, the simulated playback distance did not significantly affect the absolute angular deviation of either *H. arborea* or *P. fuscus*. In addition, the simulated broadcast dis-

tance did not influence the immobility in *P. fuscus*. Instead, the strongest patterns were associated with the weather conditions: angular deviation in *H. arborea* increased with the temperature; whereas immobility in *P. fuscus* increased with the humidity. These results suggest that short-term behavioural responses in the arena were shaped more by the abiotic conditions and individual-level variation than by the experimentally simulated distance of the acoustic stimuli. Previous studies have shown that spatial separation and signal attenuation are known to shape acoustic interactions in anurans. Bee (Bee 2012) demonstrated that frogs can distinguish between individual callers and adjust their responses based on spatial cues; while Grafe (Grafe 2005) suggested that the distance between callers modulates both competitive and reproductive signalling. Brzoska (Brzoska *et al.* 1982) showed that high-intensity playback (simulating a nearby com-

Table 3

Fixed-effect estimates from GLMMs with the Gamma error (angular deviations) and binomial error (immobility of *P. fuscus*). The intercept indicates reference levels (Broadcast distance equaling 50 m for *H. arborea* and 5 m for *P. fuscus*). Significance: * $p < 0.05$; *** $p < 0.001$.

Model	Term	Estimate	Std. Error	z value	p-value	Signif.
<i>Hyla arborea</i> – absolute angular deviations	(Intercept)	0.921	2.582	0.357	0.721	
	Time	0.038	0.040	0.943	0.346	
	Broadcast distance: 100 m	-0.145	0.468	-0.309	0.757	
	Broadcast distance: 200 m	-0.802	0.476	-1.685	0.092	
	Temperature	0.169	0.075	2.252	0.024	*
	Humidity	0.008	0.024	0.348	0.728	
<i>Pelobates fuscus</i> – absolute angular deviations	(Intercept)	4.391	3.954	1.111	0.267	
	Time	-0.003	0.027	-0.110	0.913	
	Broadcast distance: 10 m	-0.232	0.492	-0.471	0.638	
	Broadcast distance: 40 m	-0.542	0.516	-1.050	0.294	
	Temperature	0.050	0.135	0.367	0.714	
	Humidity	-0.010	0.030	-0.327	0.744	
<i>Pelobates fuscus</i> – immobility	(Intercept)	-57.424	25.980	-2.211	0.027	*
	Time	0.363	0.259	1.398	0.162	
	Broadcast distance: 10 m	0.038	1.208	0.031	0.975	
	Broadcast distance: 40 m	0.009	1.127	0.008	0.993	
	Temperature	-0.590	0.903	-0.653	0.513	
	Humidity	0.726	0.182	3.985	<0.001	***

petitor) can delay or alter male responses, suggesting that close-range signals may trigger an assessment or avoidance rather than overt aggression. Similarly, Friedl and Klump (Friedl & Klump 2002) noted that *H. arborea* males do not defend strict territories, but instead rely on graded vocal interactions influenced by the perceived rival distance. The absence of significant responses in *P. fuscus* should be interpreted cautiously given the predominance of females in the sample; thus, there was likely differences in behavioural motivation between the two species (Seglie *et al.* 2013).

The lack of response to playback calls may have resulted from several reasons. Although the playback stimuli were carefully calibrated, the physical loudspeaker was always located at the same distance from the arena, and only the apparent distance was modified acoustically. Thus, the frogs may have perceived the calls as conspecific signals, but may not have interpreted the differences among the treatments as biologically meaningful differences in distance requiring a position change. Another possible explanation is that phonotactic responses are strongly context dependent. In natural breeding aggregations, frogs receive multiple cues simultaneously, including calls from several males, background chorus

noise, substrate and vegetation cues, and possibly visual or chemical information (Starnberger *et al.* 2014). In the arena, the individuals were isolated from this broader social and environmental context. Consequently, their behaviour may have reflected exploratory movement, escape tendencies, stress after handling or general activity rather than directed phonotaxis.

For *H. arborea*, the absolute angular deviation increased significantly with the temperature. Because larger deviation values indicate a movement farther from the loudspeaker sector, this pattern suggests that the individuals were less oriented toward the playback source, or were more likely to occupy non-source sectors, at higher temperatures. This does not necessarily mean that a higher temperature caused avoidance of the playback. Instead, the temperature may have increased the frogs' general locomotor activity, making individuals more likely to move around the arena rather than remain close to the sector aligned with the loudspeaker. Moreover, *H. arborea* may actively seek cooler microhabitats in shaded areas in order to avoid critical heat thresholds (Meek 2011).

The positive effect of humidity on immobility in *P. fuscus* was counterintuitive. Individuals were more likely to remain in the centre of the arena under more

humid conditions. A higher level of humidity often facilitates amphibian surface activity by reducing the desiccation risk and enhancing the respiration rate (Riddell *et al.* 2024). However, in the context of our experiment, immobility may not represent inactivity alone, but also a tolerance to exposure in the centre of the arena. Under drier conditions, the individuals may have been more motivated to move, possibly as an escape or shelter-seeking response. In contrast, the high humidity may have reduced the immediate need to seek more favourable microhabitats, allowing the individuals to remain stationary. For a fossorial species such as *P. fuscus*, whose behaviour is closely linked to moisture conditions, the humidity may therefore have influenced a general movement tendency more strongly than the acoustic stimulation (Yermokhin *et al.* 2017).

Our results have implications for understanding spatial organisation and population structures. We do not exclude the importance of conspecific soundscapes in conveying both attractive and inhibitory information; however, the environmental conditions may be the primary factor affecting the activity of amphibians. Thus, using the playback of conspecific calls in promoting the colonisation of restored habitats (Buxton *et al.* 2015) should be also accompanied by meeting the appropriate weather conditions.

Study limitations

In this experiment, we assumed that each doubling of the distance from the sound source would result in a 6 dB decrease in the sound pressure level (SPL), consistent with the inverse-square law of attenuation under free-field conditions. This assumption is supported by strong sound absorption by vegetation at higher frequencies and the lack of major reflecting surfaces other than the ground, as has been confirmed in additional field tests. However, if the sound propagation in the study area resembled partially or fully reverberant conditions (e.g. near forest edges, buildings, irregular terrain, water surfaces or temperature inversions), then the more distant simulated calls would effectively correspond to even greater real distances than estimated.

To simulate an increased source distance, only level adjustments were applied to the playback stimuli (along with recording- and playback-chain equalisation). Artificial reverberations or echoes – typical of naturally distant calls – were intentionally excluded to avoid introducing uncontrolled effects on the behavioural responses and confounding the results.

An important limitation of our study was the difference in sex composition between the samples of

the two species. All the tested *H. arborea* individuals were males, whereas most of the tested *P. fuscus* individuals were females. Consequently, the lack of response may likely reflect different behavioural contexts. In *Hyla arborea*, advertisement calls may serve not only to attract females but also to mediate the interactions among calling males. Males respond to conspecific calls and adjust their behaviour according to the perceived social environment (Brzoska *et al.* 1982; Friedl & Klump 2002). Consequently, movements toward or away from a playback source may be balances basing on the assessment of potential competitors and the spatial organisation of breeding aggregations. In contrast, the *P. fuscus* potential responses to conspecific advertisement calls may reflect behavioural mechanisms different from those operating in male *H. arborea*, including mate-location or mate-assessment processes, which are commonly found in anurans (Seglie *et al.* 2013). Therefore, our results should be interpreted primarily as species-specific rather than as directly comparable behavioural processes between the species.

Acknowledgements

We are grateful to two anonymous referees for their constructive criticism of earlier versions of the manuscript.

Data Availability Statement

The data supporting the findings of this study has been attached as a Supplementary file.

Funding

Michał Belcik was supported by the Preludium 15 Research Grant No. 2018/29/N/NZ8/01717 from the National Science Centre in Poland.

Author Contributions

Research concept and design: M.B., P.S.; Collection and/or assembly of data: M.B., B.W., P.W.; Data analysis and interpretation: M.B.; Writing the article: M.B.; Critical revision of the article: B.W., P.W., P.S.; Final approval of article: M.B., B.W., P.W., P.S.

Conflict of Interest

The authors declare no conflict of interest.

Supplementary Materials

Supplementary Materials to this article can be found online at:

<https://www.isez.pan.krakow.pl/en/fovia-biologica>

Supplementary files:

SM.01. Data.xlsx. Dataset containing the results obtained from the experiment.

SM.02. Scripts_revised_2.R. R script containing the code used to conduct the statistical analyses.

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