1 **baRulho: an R package to quantify degradation in animal acoustic signals**

2

3 **Abstract**

4 1. Animal acoustic signals are shaped by selection to convey information based on their tempo,

5 intensity, and frequency. However, sound degrades as it propagates over space and across

6 physical obstacles (e.g., vegetation or infrastructure), which affects communication potential.

7 Therefore, transmission experiments are designed to quantify change in signal structure in a given

8 habitat by broadcasting and re-recording animal sounds at increasing distances.

9

10 2. We introduce 'baRulho', an R package designed to simplify the implementation of sound

11 transmission experiments. We highlight the package features with a case study testing the effects

12 of habitat and acoustic structure on signal transmission. Synthesized sounds that varied in

13 frequency, duration, and frequency and amplitude modulation were broadcast and re-recorded at

14 five increasing distances in open and closed understory at the Bosque de Tlalpan, Mexico City.

15 With this data, we showcase baRulho's functions to prepare master sound files, annotate re-

16 recorded test sounds, as well as to calculate and visualize measures that quantify degradation of

17 acoustic signals in the time and frequency domain.

18

19 3. Degradation measures in baRulho adequately quantified acoustic degradation, following

20 predicted patterns of sound transmission in natural environments. Re-recorded signals degraded

21 less in open habitats compared to closed habitats, with higher-frequency sounds exhibiting more

22 degradation. Furthermore, frequency modulated sounds degraded to a greater extent than pure

23 tones. The increased attenuation and reverberation observed in higher frequency sounds and

24 closed habitats suggest that factors such as absorption and scattering by vegetation play

25 significant roles in transmission patterns.

26

27 4. The R package 'baRulho' provides an open-source, user-friendly suite of tools designed to

28 facilitate analysis of animal sound degradation. Notably, it offers similar results to other sound

29 analysis software but with significantly reduced processing time. Moreover, the package

30 minimizes the potential for user error through automated test file annotation and verification

31 procedures. We hope that baRulho can help enhance accessibility to transmission experiments

32 within the research community, ultimately contributing to a deeper understanding of the

33 ecological drivers of animal communication systems.

34

37

38 **1. Introduction**

39 Acoustic signals serve as a key means through which many animals convey information and

40 navigate their social and ecological landscapes. Animal sounds are finely tuned by natural

41 selection to maximize their effectiveness within specific ecological contexts (Bradbury &

42 Vehrencamp 2011). This selective process, which acts on acoustic signals, is closely linked to the

43 propagation of sound through natural environments and the challenges it entails. Transmission in

44 natural settings can substantially impact signal integrity, potentially affecting their likelihood of

45 detection and the successful transfer of information (Morton 1975; Marten & Marler 1977). As such,

46 detailed insights into the complex interplay between animal acoustic signals and the environment,

47 are critical to further our understanding of the mechanistic basis in the evolution of acoustic

48 communication (Endler 1992; Cardoso & Price 2010; Tobias et al. 2010).

49   Sound transmission experiments are a key tool to evaluate the interaction of signals with a

50   callers' natural environment. Transmission studies seek to test hypotheses related to the

51   degradation of sounds over space in combination with environmental factors that may influence

52   selection on signal form and function (Graham et al. 2017; Benedict et al. 2021). Typically, this is

53   achieved by broadcasting and re-recording animal sounds or synthesized sounds at increasing

54   distances. Next, changes to the structural components of sounds are quantified by measuring

55   modification to the power distribution in time and frequency domains and on combined time-

56   frequency representations of sound (reviewed by Hardt & Benedict 2020). Such experiments have

57   provided valuable insight into factors that affect signal transmission in natural environments. For

58   instance, both habitat and acoustic structure can affect transmission in a significant manner

59   (Kime et al. 2000; Apol et al. 2017; Wheeldon et al. 2022). In addition, other factors such as

60   anthropogenic noise masking (Leader et al. 2005; LaZerte et al. 2015; Grabarczyk & Gill 2020),

61   distance of the signaler from the ground, which leads to additional attenuation (Balsby et al. 2003;

62   Darden et al. 2008; Arasco et al. 2022), as well as ambient temperature, humidity, and wind speed

63   (Bradbury & Vehrencamp 2011), which also influence transmission patterns.

64   Conducting sound transmission experiments, however, can be challenging. Several steps

65   are involved, such as careful formatting and manipulation of audio files, broadcasting and re-

66   recording study signals in natural settings, annotation of re-recorded files, and quantification of

67   degradation measures. These difficulties have likely contributed to the limited implementation of

68   such experiments in animal communication research. Here, we introduce the R package 'baRulho'

69   (Portuguese for 'noise'), which is intended to facilitate animal sound transmission experiments

70   and their subsequent analysis. The package offers tools to help researchers at each step of the

71   process, from generating synthesized sounds and creating playback sound files, to streamlining

72   annotation and measurement of sound degradation in re-recorded signals. We highlight package

73   features with a case study testing the effects of habitat and signal structure on transmission

74 properties using synthesized sounds. In addition, as proof of concept, we compared baRulho's

75 output to that of Sigpro (Pedersen 1998), the most commonly used software for quantifying

76 animal sound degradation.

77

78 **2. Implement transmission experiments with baRulho**

79

80 Sound transmission experiments often follow a common sequence of stages (Table 1). The

81 baRulho package offers a variety of functions to assist users during most stages. We showcase the

82 package in an analysis workflow with our case study testing the effects of habitat and acoustic

83 signal structure on sound transmission.

84

85

86 *Table 1. Common steps in sound transmission experiments and associated functions in the baRulho*

87 *package. For functions that compute degradation measures, which are listed under the 'Quantify*

88 *degradation' stage, the "Description" field includes an explanation of the computed measure as well*

89 *as selected citations to studies that employ the measure. Model sounds: sound in which degradation*

90 *will be measured, usually found in the original field recordings or synthesized sound files. Reference*

91 *sounds: sounds to use as a template to compare against for measuring degradation (typically re-*

92 *recorded at 1 m). Test sounds: sounds re-recorded during playback experiments.*

93

Experimental stage	Function	Description
Obtain signals / Synthesize sounds	*synth_sounds()*	Creates synthesized sounds that can be used for playback experiments. Can add variation to signal structure in five features: frequency, duration, harmonic structure, frequency modulation, and amplitude modulation.
Create master sound file for playback	*master_sound_file()*	Creates a sound file for playback experiments by clipping model sounds from one or more sound files and concatenating them in a single sound file, adding acoustic markers at the start and end to simplify time syncing of test sounds.

Time sync re-recorded sounds	find_markers()	Finds the time location of acoustic markers in the test sound files in order to time sync test sounds.
	align_test_files()	Uses the time location of acoustic markers (determined by find_markers()) to determine the location of test sounds.
	auto_realign()	Automatically adjusts the start and end of individual test sounds using spectrogram cross-correlation.
	manual_realign()	Interactive graphic device to manually adjust the start and end of test sounds.
	plot_aligned_sounds()	Creates image files with spectrograms to visually inspect alignment precision on test sound files (as single panels in Fig. 1).
Quantify degradation	blur_ratio()	Measures the mismatch between amplitude envelopes (expressed as probability mass functions) of reference and test sounds. By converting envelopes to probability mass functions the effect of power attenuation is removed, focusing the analysis on the modification of envelope shape. Higher values indicate more degradation. See also plot_blur_ratio() for visual inspection of blurring (Dabelsteen et al. 1993; Brown & Handford 2003, Fig. 3).
	envelope_correlation()	Measures the similarity between reference and test sounds as the Pearson correlation between the two amplitude envelopes. Lower values indicate more degradation.
	excess_attenuation()	Measures additional amplitude loss between reference and test sounds that is greater than expected due to spherical spreading. Represents power loss due to additional factors like vegetation or atmospheric conditions. Higher values indicate more degradation (Holland et al. 1998; Darden et al. 2008).
	signal_to_noise_ratio()	Measured as the ratio of sound power level of test sounds to that of ambient noise. Sound power measured as the root-mean-square of the amplitude envelope. Lower values indicate more degradation (Dabelsteen et al. 1993; Blumenrath & Dabelsteen 2004).
	spcc()	Spectrographic cross-correlation between reference and test sounds as a measure of distortion in a time-frequency representation of sound. Computed as the maximum Pearson correlation from a sliding window procedure on Fourier or auditory scale spectrograms.
	spectrum_blur_ratio()	Measures the mismatch between power spectra (expressed as probability mass functions) of reference and test sounds. Equivalent to blur_ratio() but in the frequency domain. Higher values indicate more degradation. See also plot_blur_ratio(..., type = "spectrum") for visual inspection of blurring.
	spectrum_correlation()	Measures the similarity between reference and test sounds as the Pearson correlation between two power spectra. Equivalent to spectrum_correlation() but in the frequency domain. Lower values indicate more degradation.
	tail_to_signal_ratio()	Measures the ratio of power in the tail of reverberations (found immediately after the sound) to that of the test sounds. Sound power is measured as the root-mean-square of the amplitude envelope. Higher values indicate more degradation (more reverberation) (Dabelsteen et al. 1993; Nemeth et al. 2006).
	plot_degradation()	Creates multipanel plots (as image files) with spectrograms, amplitude envelopes, and power spectra of reference and test sounds, arranged by distance and transect to simplify visual assessment of degradation (as in Fig. 2).

94

95

2.1. Case study: effects of habitat and signal structure on transmission

We conducted a sound transmission experiment to evaluate the effects of habitat and signal structure on degradation of synthesized sounds. Experiments were conducted on March 3, 2020 at Bosque de Tlalpan, Mexico City, an urban park composed of a mixture of xeric shrubland and oak forest. Reference sounds were recorded in open habitat (described below) at a mean sound pressure level of 82 dB, fast averaging, measured at 1 m from the playback speaker (Bose color soundlink). Test sounds were recorded along a transect at 10, 30, 65, and 100 m from the speaker with a Audio-Technica ATR6550X microphone and a Zoom H4n Pro recorder (44.1 kHz sampling rate, 16 bit amplitude resolution, WAV format). Both the microphone and speaker were placed horizontally at 2 m above ground, attached to vertical poles. Playbacks were conducted at three locations within the park. At each location, we broadcast sounds over one transect in habitat with open understory (a cleared walking path with no vegetation between the speaker and microphone) and an adjacent transect in habitat with closed understory (regular vegetation between the speaker and microphone). The order of the transects (open and closed) was alternated.

Synthesized sounds

We used the baRulho function *synth_sounds* to create synthesized sounds that varied in four structural features: frequency (20 values between 0.5 and 10 kHz, every 0.5 kHz), duration (0.1 s and 0.2 s), frequency modulation (pure tones versus frequency modulated sounds, simulated with a brownian bridge motion stochastic process), amplitude modulation (flat amplitude envelopes versus two amplitude peaks with a value 4 times that of the lowest amplitude). We synthesized sounds representing all possible combinations of signal structure with the four varying features, which resulted in 160

121   unique sounds. Each structure was replicated three times for a total of 480 sounds in the

122   master sound file.

123

```
synth_data <-
       synth_sounds(
       replicates = 3, # number of replicates for each feature combination
       frequencies = seq(0.5, 10, length.out = 20),
       durations = c(0.2, 0.1),
       am = TRUE, # amplitude modulation
       fm = TRUE, # frequency modulation
       sig2 = 0.8, # frequency modulation parameter
       shuffle = TRUE # randomize the position of sounds
       )
```

124
125
126   The position of sounds in the master sound file was randomized to avoid adjacent replicates

127   (argument *shuffle* = TRUE). This helps to avoid clustering samples for a given treatment within the

128   master file, which may be affected by fluctuations or irregularities of ambient sounds that mask

129   test sounds during playback experiments. The amount of modulation can be adjusted with the

130   argument *sig2*, which controls the magnitude of frequency change at each step in the brownian

131   motion process. The output of *synth_sounds()* can be used by the function *master_sound_file()* to

132   create a master sound file for playback experiments (i.e. a sound file with all the model sounds in

133   which transmission will be quantified). This function concatenates all sounds into a single sound

134   file, adding silence between sounds (argument *gaps*). In addition, the function adds two acoustic

135   markers at the start and end of the sound files to allow for automated annotation of the re-

136   recorded test files (hereafter test files, explained below; FIG W):

137

```
master_annotations <- master_sound_file(X = synth_data, # synthesized sound data
       file.name = "master",  # name of the sound file
       gap.duration = 0.2) # duration of silence in between sounds
```

138

139   The result is a WAV file added to the current working directory and a data frame with annotations

140   (i.e. time-frequency location) of sounds in the WAV file. The *master_sound_file* function normalizes

141   the amplitude to ensure all sounds have the same maximum amplitude. This function can also be

142   used to create master sound files from annotated animal (non-synthesized) sounds.

143

144   *Time-sync test files*

145

146   Following playback experiments, the next step is to accurately determine the time location of

147   each test sound among recordings. Without proper alignment, time mismatches between test and

148   reference sounds can produce inaccurate results. Traditionally, the position of test sounds has

149   been determined by visual inspection of waveforms, which can be prone to user error. The

150   package baRulho offers several functions to align recordings in a more systematic way. The

151   function *find_markers* uses spectrographic cross-correlation to locate, in test files, the start and

152   end acoustic markers added by *master_sound_file*. Because the time difference between sounds

153   remains constant, the position of sounds in the test files can be inferred by determining the

154   position of any of the sounds. In this case, the structure of the start and end markers, with higher

155   amplitude (twice that of test sounds by default) and low frequency (2 kHz median frequency by

156   default) make them less prone to degradation during transmission and therefore more likely to be

157   accurately located after being re-recorded. The following code finds acoustic markers over all test

158   sounds from our experiment, which have been shared in the supplementary materials:

159

```r
# directory path where supplementary files have been saved
options(sound.files.path = "PATH_TO_FILES")

markers_in_tests <-
        find_markers(X = master_annotations) # annotations in master file

# print output
```

```
head(markers_in_tests)
```

sound.files	selec	start	end	scores	marker	time.mismatch
trnsc1_100m_closed.wav	1	6.049203	7.049203	0.2227792	start_marker	0.0300544
trnsc1_100m_closed.wav	2	257.700686	258.700686	0.2726756	end_marker	NA
trnsc1_100m_open.wav	3	29.502300	30.502300	0.7150524	start_marker	0.0131017
trnsc1_100m_open.wav	4	281.136830	282.136830	0.6083450	end_marker	NA
trnsc1_10m_closed.wav	5	39.452253	40.452253	0.7046298	start_marker	0.0114997
trnsc1_10m_closed.wav	6	291.085182	292.085182	0.8364759	end_marker	NA

161
162   The output contains time-frequency coordinates of the start and end markers for each test file. In

163   addition, the output also contains a 'time.mismatch' column that compares the time gap between

164   the two markers in the test files against that in the master sound file. For perfect detection the

165   value must equal 0, therefore, this number can be used as a measure of the maximum possible

166   error. The output from *find_markers* can then be used by the function *align_test_files* to determine

167   the location of all other test sounds:

168

```
aligned_tests <-
        align_test_files(X = master_annotations, # annotations of sounds in master file
                Y = markers_in_tests) # position of markers in test files

# print output
aligned_tests
```

169

sound.files	selec	start	end	bottom.freq	top.freq	sound.id	marker
trnsc1_100m_closed.wav	1	6.060.315	7.060.315	1.333.333	2.666.667	start_marker	end_marker

sound.files	selec	start	end	bottom.freq	top.freq	sound.id	marker
trnsc1_100m_closed.wav	2	7.110.315	7.310.338	7.875.000	8.805.000	dur:0.2;freq:9;fm;am_1	end_marker
trnsc1_100m_closed.wav	3	7.360.338	7.560.361	3.208.000	4.069.000	dur:0.2;freq:4;fm;am_1	end_marker
trnsc1_100m_closed.wav	4	7.610.361	7.810.383	0.422000	1.223.000	dur:0.2;freq:1;fm;am_1	end_marker
trnsc1_100m_closed.wav	5	7.860.383	8.060.406	6.905.000	7.917.000	dur:0.2;freq:7;fm;am_1	end_marker
trnsc1_100m_closed.wav	6	8.110.406	8.310.429	8.417.000	9.416.000	dur:0.2;freq:9.5;fm;am_1	end_marker

170

171 The function *align_test_files* uses the marker with the highest cross-correlation to estimate the

172 location for all other sounds in the test files. In cases where the location of test sounds (i.e.

173 individual sounds in test files) is still slightly off, sounds can be further aligned with the functions

174 *auto_realign* and *manual_realign* (Table 1). The output of *align_test_files,* (and from *auto_realign*

175 and *manual_realign*) contains the time-frequency coordinates for all test sounds (Fig. 1). The

176 precision of the alignment can be visually inspected using the function *plot_aligned_sounds*,

177 which produces images similar to the spectrograms in each individual panel in Figure 1.
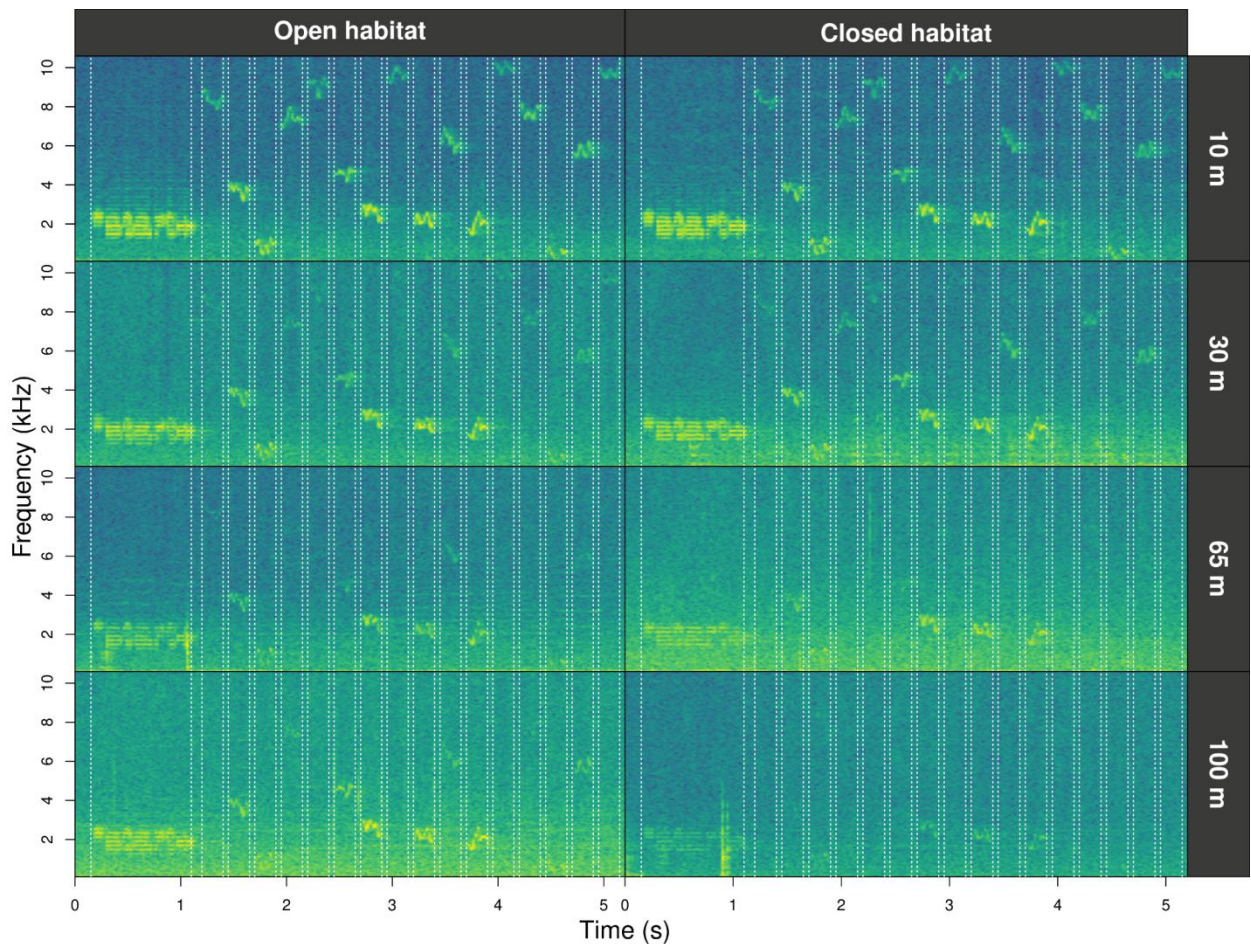
178

179

Figure 1. Fourier spectrograms of test recordings from an experimental transect in open and closed

habitats (columns) re-recorded at four distances from the playback speaker (rows). The dotted

vertical lines highlight the detected position of sounds computed by the functions find_markers and

align_test_files.

Alignments can be further adjusted manually with the function *manual_realign*. The function

generates a multipanel graph with a spectrogram of the master sound file on top of that from test

sound files. This highlights the position of correspondent test sounds on both in order to assess

and adjust alignment. The lower spectrogram shows a series of 'buttons' that users can click on to

control the time position of test sound files:

```
realigned_tests <- manual_realign(
    X = aligned_tests, # test file annotations
```

```
         Y = master_annotations, # master sound file annotations
              marker = "end_marker", # marker to focus on
         flim = c(0, 6)) # frequency range limits
```

191

192   The function returns an object similar to the input test file annotations in which the start and end

193   of the sounds have been adjusted based on user input. The format of annotations is shared by

194   other bioacoustics R packages, which enables the use of additional functionalities, like exporting

195   annotations to external software for further inspection (Rraven, Araya-Salas 2017) or signal

196   structure quantification and additional visualizations (warbleR; Araya-Salas & Smith-Vidaurre

197   2017).

198

199   The last stage of analysis involves the quantification of sound degradation. Most degradation

200   measures require a comparison between test sounds that were recorded at different distances

201   from the speaker, to their reference, which is often re-recorded at 1m. Hence, a column that

202   indicates the distance at which each sound was recorded is needed. The function

203   *set_reference_sound*s determines annotation to be used as reference for each test sound:

204

```
# get distance
realigned_tests$distance <- sapply(strsplit(realigned_tests$sound.files,
   "_"), "[[", 2)

# make it a numeric column
realigned_tests$distance <- as.numeric(gsub("m", "", realigned_tests$distance))

# set reference sounds
test_data <- set_reference_sounds(realigned_tests, method = 1)
```

205

206   If the default method is used ('method = 1'), the reference is determined as the re-recorded sample

207   of a sound recorded at the shortest distance. The function adds a column "reference" that is used

208   by functions for measuring degradation. We use the output of this function to compute all eight

209   degradation measures available in baRulho (Table 1). Here, we present the code for four such

210   measures to show how easily they can be obtained with baRulho:

211

```
# get degradation measures each one in a line of code
degrad_df <- blur_ratio(aligned_tests)

degrad_df <- excess_attenuation(degrad_df)

degrad_df <- signal_to_noise_ratio(degrad_df,
            mar = 0.1) # mar = margin to measure noise

degrad_df <- tail_to_signal_ratio(degrad_tests, mar = 0.1) # mar = margin to measure tail

# or as a pipe
degrad_df <- aligned_tests |>
        excess_attenuation() |>
        signal_to_noise_ratio(mar = 0.1) |> # mar = margin to measure noise
        blur_ratio() |>
        tail_to_signal_ratio(mar = 0.1) # mar = margin to measure tail


head(degrad_df) # print the first 6 rows
```

212

sound.files	selec	sound.id	distance	reference	excess.attenuation	signal.to.noise.ratio	blur.ratio	tail.to.signal.ratio
trnsc1_100m_closed.wav	2	dur:0.2;freq:9;fm;am_1	100	trnsc1_1m_open.wav-2	8.999.975	0.7685672	0.2920241	-0.9995171
trnsc1_100m_closed.wav	3	dur:0.2;freq:4;fm;am_1	100	trnsc1_1m_open.wav-3	10.829.675	0.6384587	0.2976129	0.1901690
trnsc1_100m_closed.wav	4	dur:0.2;freq:1;fm;am_1	100	trnsc1_1m_open.wav-4	26.216.040	45.246.601	0.1418792	24.441.865
trnsc1_100m_closed.wav	5	dur:0.2;freq:7;fm;am_1	100	trnsc1_1m_open.wav-5	15.191.104	-13.816.010	0.2667528	0.0593048

| trnsc1_100m_closed.wav | 6 | dur:0.2;freq:9.5;fm;am_1 | 100 | trnsc1_1m_open.wav-6 | 6.041.307 | -0.2574492 | 0.2059137 | -12.052.163 |
| trnsc1_100m_closed.wav | 7 | dur:0.2;freq:4.5;fm;am_1 | 100 | trnsc1_1m_open.wav-7 | 12.278.579 | -0.7122037 | 0.2213225 | 16.697.592 |

213

214

215 The output includes measures of degradation for each test sound (time and frequency position

216 columns are excluded for simplicity). Measurements that involve a comparison between test and

217 reference sounds do not return a value for the reference sounds (recorded at 1m). All functions

218 compute degradation measures within the frequency range of model sounds provided in the

219 annotations used for creating the master sound file. To analyze transmission patterns, we

220 constructed a measure of "overall degradation" based on all eight degradation measures (Table 1),

221 computed as the first component of a Principal Component Analysis on zero-mean, unit variance

222 degradation measures.

223

224 Sound degradation at increasing distances can be visually inspected with the function

225 *plot_degradation.* This function produces JPEG files with a mosaic of visual representations of

226 sounds (Fourier spectrograms, power spectrum, and amplitude envelopes) for each test sound

227 and corresponding reference sound (Fig. 2):

228

```
# get directory to save images
options(dest.path = "DIRECTORY_TO_SAVE_IMAGE_FILES")
plot_degradation(X = test_data)
```
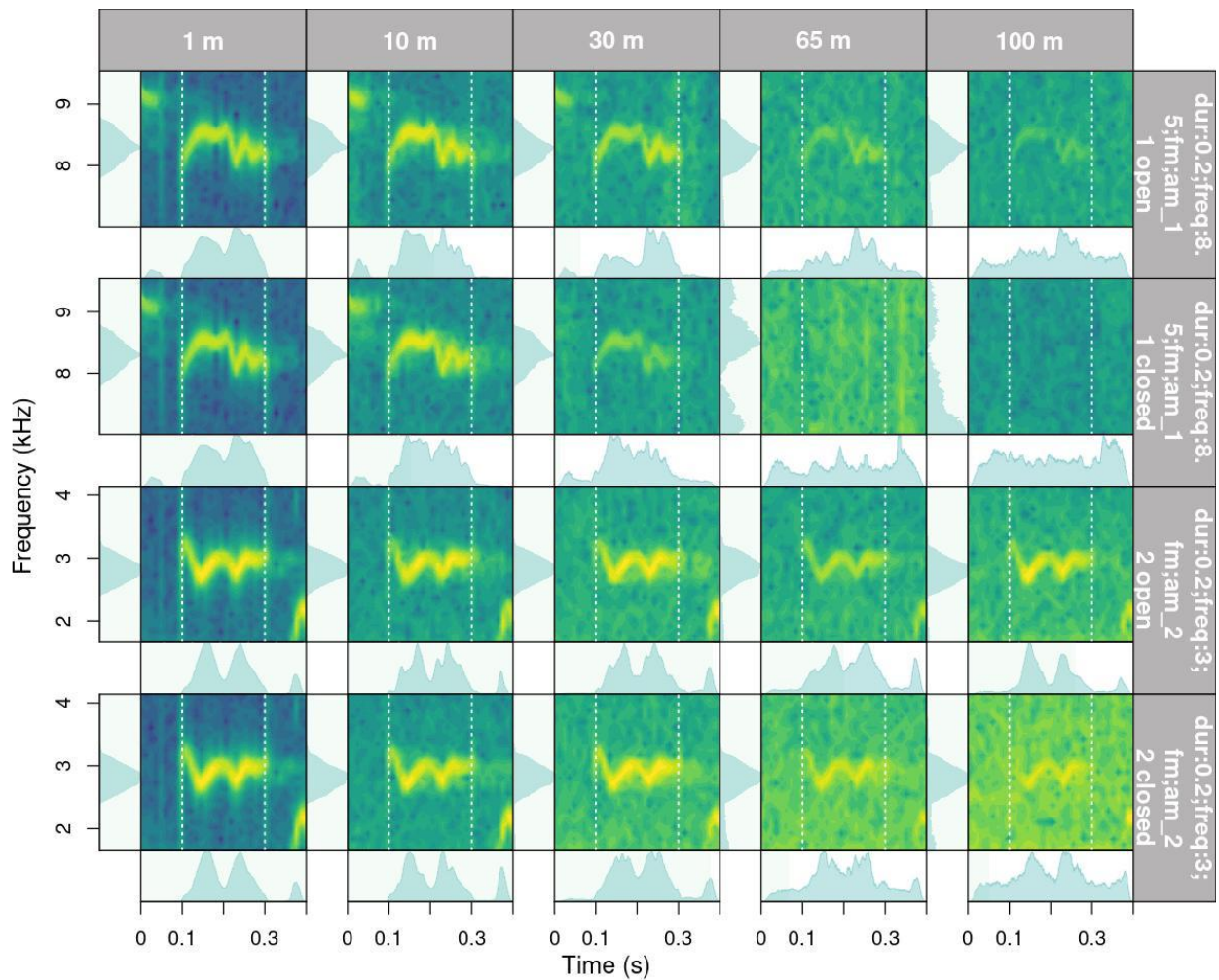
229

Figure 2. Output from function plot_degradation that shows the Fourier spectrogram, amplitude

envelope, and power spectrum for test sounds (distances 10, 30, 65 and 100 m) and their

corresponding reference sound (1 m). The first and second row contain a 0.2 s long, 8.5 kHz,

frequency and amplitude modulated sound recorded in open and closed understory, respectively.

The third and fourth row contain a 0.2 s long, 3 kHz, frequency and amplitude modulated sound

recorded in open and closed understory.

The function *plot_blur_ratio* can also be used to visually inspect degradation, which creates JPEG

image files with spectrograms of the reference and test sounds (one image for each test sound)

and the overlaid power distribution (either amplitude envelopes or power spectrum, see

argument 'type') as probability mass functions (Fig. 3). The output graphs highlight the mismatch

242 between the two compared distributions (reference and test), which represents the computed

243 blur ratio returned by either *blur_ratio* or *spectrum_blur_ratio*.

244

```
plot_blur_ratio(X = test_data)
```
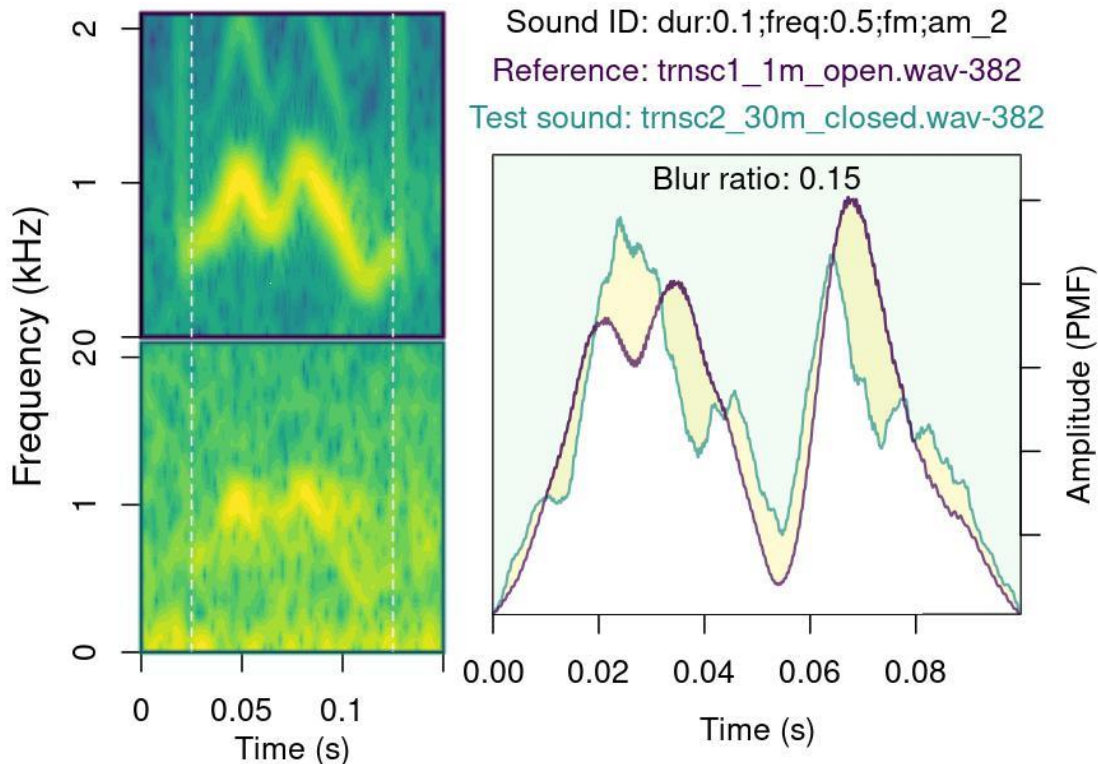
245

246
247 *Figure 3. Output from plot_blur_ratio that shows spectrograms of the reference and test sound, the*

248 *overlaid amplitude envelopes, and the mismatch between the two (yellowish area between the*

249 *reference [purple line] and test sound [green line]).*

250

251 2.2 *Statistical Analysis*

252

253 *Patterns of signal degradation*

254

255 We used Bayesian regression models to evaluate the effect of sound structural features (frequency,

256 frequency modulation, amplitude modulation, and duration) and habitat structure on four

257   degradation measures: blur ratio, excess attenuation, tail-to-signal ratio, and overall degradation

258   (PC1). Models included interaction terms between habitat structure and each of the sound

259   structural features. Distance was modeled as a monotonic effect in which distance levels are not

260   assumed to be equidistant with respect to their effect on the response variable, rather are

261   estimated from the data (Bürkner & Charpentier 2020). Frequency was mean-centered and scaled

262   by dividing it by two standard deviations to allow direct comparisons between effect sizes from

263   categorical predictors (Schielzeth 2010; Gelman 2008). Single response regressions were run for

264   each of the degradation measures. Regressions were run in Stan (Stan Development Team 2021)

265   through the R package brms (Bürkner 2017). Response variables were modeled with a normal

266   distribution. Transect and sound replicates were included as varying intercept effects to account

267   for the paired nature of transects and the non-independence of observations, respectively. Effect

268   sizes are presented as median posterior estimates and 95% credibility intervals as the highest

269   posterior density interval. Minimally informative priors were used for population-level effects

270   (normal distribution; mean = 0; SD = 2) and their standard deviation (Cauchy distribution; median

271   = 0; scale = 4). Predictors in which credible intervals did not include zero were regarded as having

272   an effect on the response variables. Models were run on four chains for 5000 iterations, following a

273   warm-up of 5000 iterations. The effective sample size was kept above 1500 for all parameters.

274   Performance was checked visually by plotting the trace and distribution of posterior estimates for

275   all chains. We also plotted the autocorrelation of successive sampled values to evaluate the

276   independence of posterior samples, ensured that the potential scale reduction factor for model

277   convergence was kept below 1.01 for all parameter estimates and generated plots from posterior

278   predictive samples to assess the adequacy of the models in describing the observed data

279   (Supplemental Materials).

280

281   *2.3 Comparing baRulho and Sigpro*

282

283 Sigpro (Pedersen 1998) is, to our knowledge, the only software package specifically dedicated to

284 quantifying animal sound degradation (Holland et al. 1998; Balsby et al. 2003; Lampe et al. 2007;

285 Darden et al. 2008; Barker et al. 2009; Graham et al. 2017; Vargas-Castro et al. 2017; Wheeldon et al.

286 2022). Therefore, we compared measurements extracted in baRulho and Sigpro to evaluate their

287 equivalence. In both programs, we noted the amount of time to complete each analysis.

288 Measurements were taken on a subset of the recording data that included 80 test sounds (20

289 sounds re-recorded at 4 distances). For our comparison, we used four degradation measures that

290 are included in both software packages: blur-ratio, excess attenuation, signal-to-noise ratio, and

291 tail-to-signal ratio. The analysis was run by MQO, who was already trained on both packages, on a

292 laptop computer (Lenovo, 16 GB RAM memory, Intel Core i7-1255U (1.70 GHz)). In Sigpro, we

293 tested sounds in two ways, first with the original test files, which is the default procedure in Sigpro.

294 This required manually setting the time location for test sounds within the entire re-recorded

295 sound file. In some cases manual placement is difficult, especially at the furthest recording

296 distances where some signals leave almost no trace on the spectrograms, which potentially

297 increases measurement error. Hence, we ran an additional analysis in Sigpro on individual audio

298 clips for each test sound, in which the start of the clip matched the time location used in baRulho.

299 We expected this approach would minimize measurement error, providing a more direct

300 comparison between the two software packages. We used Pearson correlation to quantify

301 agreement between degradation measures in Sigpro and baRulho.

302

303 **3. Results & Discussion**

304

305   The baRulho package streamlines the process of evaluating acoustic signal degradation, including

306   tasks that previously lacked programmatic solutions. Particularly relevant is the functionality

307   related to simulating model sounds with animal-like attributes for transmission playbacks,

308   concatenating annotated sounds into master sound files for playback experiments, and

309   automating the location of test sounds in the re-recorded sound files. The package also introduces

310   two new degradation measures (i.e. spectrum_correlation and spectrum_blur_ratio) to explore

311   and quantify patterns of sound propagation. Automated annotation, parallel computing, and

312   seamless integration of data batch processing throughout the entire workflow enhances

313   computational efficiency, facilitating analysis of large datasets.

314   Measures incorporated in the baRulho package adequately quantify acoustic degradation,

315   as the results of our case study are consistent with the observed patterns of sound degradation in

316   natural environments. We found that habitat structure (i.e. open or closed understory) was a

317   primary driver of sound degradation (Fig. 4): degradation in closed understory was more

318   pronounced than in open understory. This effect was evident on the first principal component

319   (overall degradation) as well as on three models that tested single degradation measures (blur

320   ratio, excess attenuation, and tail-to-signal ratio; Fig. 4). In closed habitats, vegetation impedes

321   signal propagation, often through scattering, which results in higher distortion (blur ratio) and

322   reverberation (tail-to-signal ratio) (Dabelsteen et al. 1993; Balsby et al. 2003). Leafy vegetation

323   may also absorb signals as they propagate through closed habitat, and as a result, leads to

324   additional loss of signal intensity or excess attenuation (Holland et al. 1998; Darden et al. 2008).

	habitat structure	frequency	duration	amplitude modulation	frequency modulation
Degradation (PC1)	1.019	1.059	0.073	0.139	-0.197
Blur ratio	0.022	0.018	0.014	0.022	0.049
Excess attenuation	7.486	13.703	0.792	-3.295	-3.427
Tail-to-signal ratio	3.27	1.622	-0.4	0.659	-0.692

P value
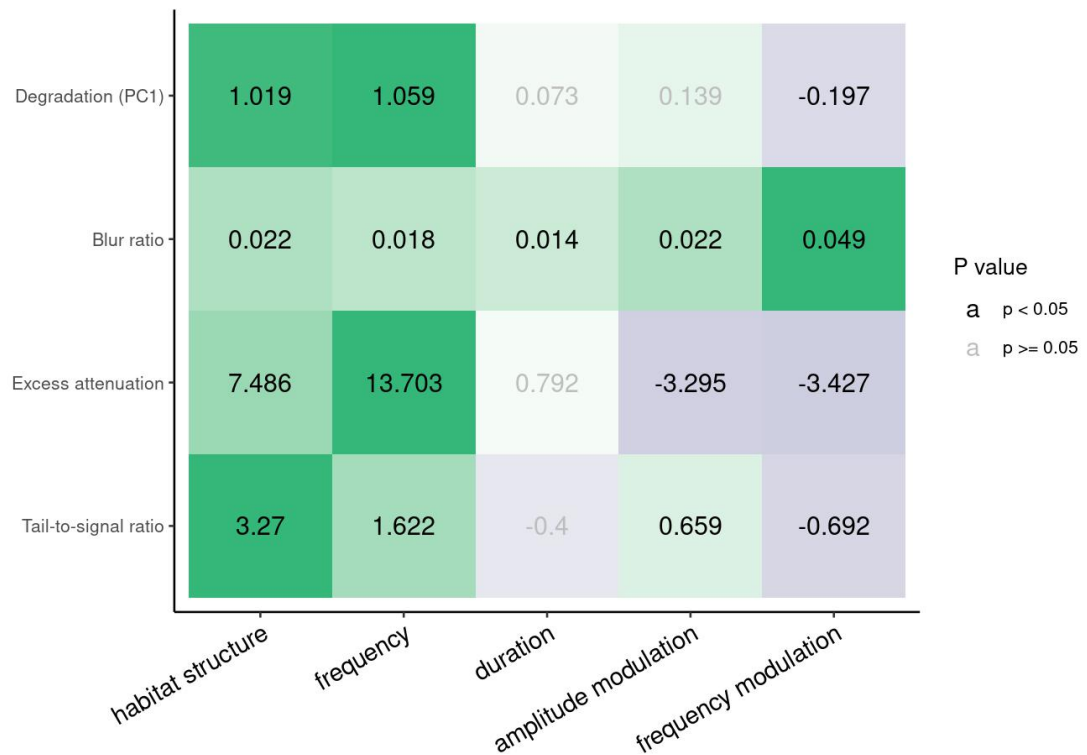a   p < 0.05
a   p >= 0.05

325

Figure 4. Effect size estimates of predictor variables representing habitat and signal structure

(columns) on the signal degradation response variables (rows). Values in gray indicate effects that

did not differ from zero. Single models were run for each response. The cell color gradient denotes

the magnitude of the effects relative to the highest effect size within a model. Green and purple colors

indicate positive and negative effects, respectively.

331

332   Frequency was the structural feature more closely linked to degradation (Fig. 4). Higher

333   frequencies show greater overall degradation, excess attenuation, reverberation, and, to a minor

334   degree, amplitude envelope blurring (Fig. 4). Low frequency sounds, due to longer wavelengths,

335   are less susceptible to scattering, thus attenuate less over distance compared to higher frequency

336   sounds (Wiley & Richards 1982). Frequency modulation and, to a lesser extent amplitude

337   modulation, contributed to distortion of the amplitude envelope (blur ratio; Fig. 4). Tonal sounds

338   withstand scattering better than frequency modulated sounds (Morton 1975; Marten & Marler

339   1977). Accordingly, low frequency, tonal sounds are often considered advantageous for long-

340   distance communication in closed habitats, such as forests, as salient information may be better

341   detected over larger distances (Yip et al. 2017). However, we also found differences in the way

342   each structural feature influenced degradation. Particularly relevant is the lower degradation,

343   attenuation and reverberation of frequency modulated sounds compared to pure tones.

344   Amplitude modulated sounds were also less attenuated than their non-modulated counterparts

345   (Fig. 4). Over distance, original patterns of amplitude modulation elicited from a sender declines

346   or blurs (Dabelsteen et al. 1993; Apol et al. 2017). Nonetheless, amplitude modulated sounds are

347   more detectable at lower signal-to-noise ratios than sounds without amplitude modulation (Lohr

348   et al. 2003), which could explain the observed pattern. Overall, our results are consistent with

349   predictions from the Acoustic Adaptation Hypothesis (AAH), which posits that habitat-dependent

350   degradation imposes a strong selective pressure on animal acoustic signals, favoring features that

351   optimize efficient transmission (Morton 1975).

352   Overall, we found agreement between baRulho and Sigpro results. Measurement

353   agreement was modest between the two software when we manually located test sounds in

354   Sigpro (tail-to-signal ratio: $r = 0.61$; signal-to-noise ratio: $r = 0.79$; blur ratio: $r = 0.5$; excess

355   attenuation: $r = 0.75$). However, agreement improved markedly when Sigpro measures were taken

356   on recording clips that started at the onset of sounds, which we determined in baRulho (tail-to-

357   signal ratio: $r = 0.8$; signal-to-noise ratio: $r = 0.94$; blur ratio: $r = 0.8$; excess attenuation: $r = 0.97$; Fig.

358   5). The observed agreement indicates that degradation measures obtained with baRulho are

359   comparable to those from Sigpro. The observed improvement when time location between

360   recordings for the Sigpro analysis was determined using the baRulho approach suggests that

361   much of the mismatch between the two software packages is due to the way sound position is

362   determined in each program. Sigpro requires visual inspection of the waveform to manually

363   identify test and reference sounds, which must be repeated even when the same reference is used

364   several times. In contrast, baRulho employs spectrogram cross-correlation to find the position of

365   acoustic markers, which are then used to compute positions for all other sounds (Fig. 1).

366   Furthermore, baRulho provides a means for identifying poor location estimates and additional

367   functionality to improve their accuracy. Spectrogram cross-correlation for signal alignment is

368   beneficial, given that this approach successfully determined the position of all test sounds, even

369   on recordings made 100 m from the speaker. Our package also represents a significant

370   improvement in computational efficiency. The analysis of the subset of 80 test sounds in Sigpro

371   took 861 min to complete. In contrast, the same analysis in baRulho took 7.43 minutes (26.65

372   seconds of computing time running the script using 8 cores), on a regular laptop computer, which

373   is approximately 119 times faster.
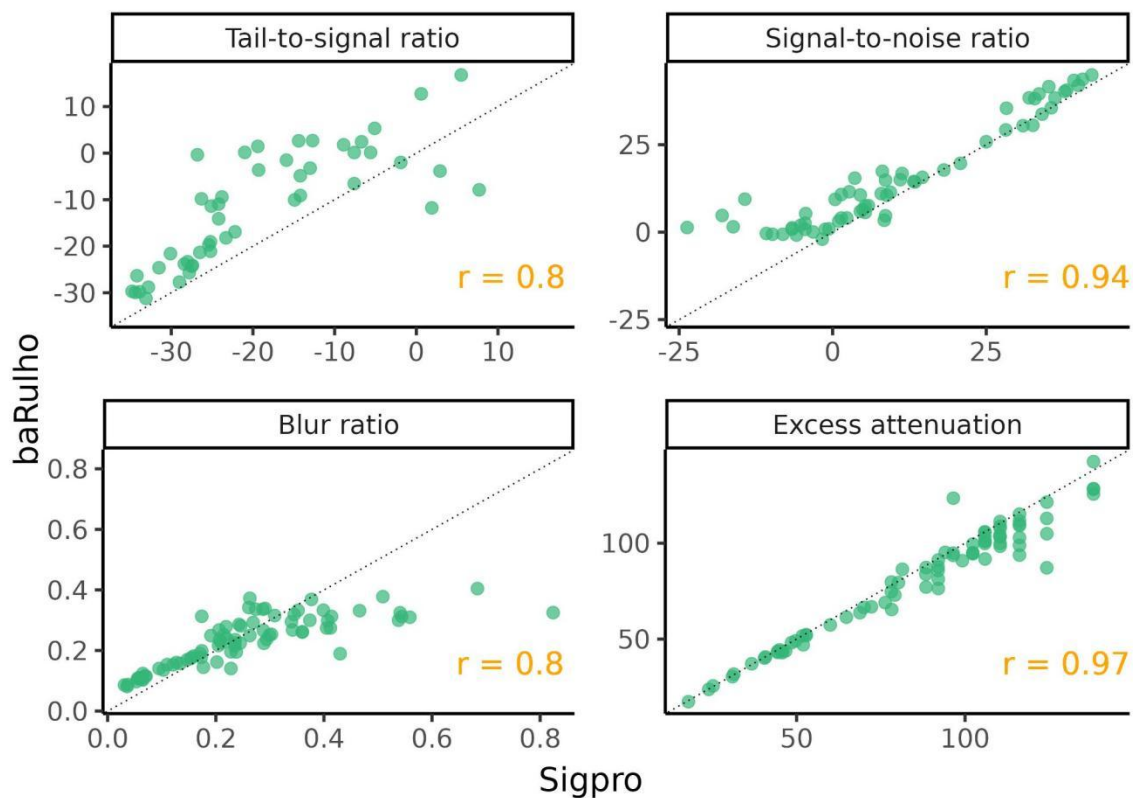
374

375

376   *Figure 5. Scatterplots showing the agreement between baRulho and Sigpro for the four degradation*

377   *measures in common. The Pearson correlation coefficient for each comparison is shown in the*

378   *bottom right corner of each panel. Sigpro measures shown were taken on recording clips that started*

379   *at the onset of sounds, which was determined in baRulho.*

380

381   **4. Conclusions**

382

383   The R package baRulho provides a user-friendly suite of tools designed to measure animal sound

384   degradation via signal transmission experiments. We show how the package can be used across

385   the different stages of a transmission experiment, from data preparation to quantification of

386   degradation. The sound analysis results generated by baRulho and Sigpro are similar, making

387   results comparable across studies using either software. However, baRulho provides significant

388   improvements to previous approaches as manual annotation is not required to determine test

389   sound location, much less time is needed to complete data extraction, new measures are added to

390   quantify novel aspects of degradation, and new visualizations are available for inspecting

391   degradation. We expect this package to be a useful contribution to the community that can enable

392   researchers to bring more detailed insight into the evolutionary processes that have shaped

393   animal acoustic communication in natural environments.

394

395   **Conflicts of Interest:** The authors declare no conflicts of interest.

396

397   **References**

398

399   Apol, C. A., Sturdy, C. B., & Proppe, D. S. (2018). Seasonal variability in habitat structure may have

400   shaped acoustic signals and repertoires in the black-capped and boreal chickadees. *Evolutionary*

401   *Ecology*, *32*, 57-74.

402

403 Arasco, A. G., Manser, M., Watson, S. K., Kyabulima, S., Radford, A. N., Cant, M. A., & Garcia, M.

404 (2022). Testing the acoustic adaptation hypothesis with vocalizations from three mongoose

405 species. *Animal Behaviour*, *187*, 71-95

406

407 Araya-Salas, M. (2017). Rraven: connecting R and Raven bioacoustic software. R package version,

408 1(2).

409

410 Araya-Salas, M., & Smith-Vidaurre, G. (2017). warbleR: an R package to streamline analysis of

411 animal acoustic signals. *Methods in Ecology and Evolution*, 8(2), 184-191.

412

413 Balsby, T., Dabelsteen, T., & Pedersen, S. B. (2003). Degradation of whitethroat vocalisations:

414 implications for song flight and communication network activities. *Behaviour*, *140*(6), 695-719

415

416 Barker, N. K., Dabelsteen, T., & Mennill, D. J. (2009). Degradation of male and female rufous-and-

417 white wren songs in a tropical forest: effects of sex, perch height, and habitat. *Behaviour*, 1093-

418 1122.

419 Benedict, L., Hardt, B., & Dargis, L. (2021). Form and Function Predict Acoustic Transmission

420 Properties of the Songs of Male and Female Canyon Wrens. *Frontiers in Ecology and Evolution*, *9*,

421 797. https://doi.org/10.3389/fevo.2021.722967

422 Bradbury, J. W., & Vehrencamp, S. L. (2011). Principles of animal communication, 2nd edn

423 Sunderland. *MA: Sinauer Associates.*

424 Brown, T. J., & Handford, P. (2003). Why birds sing at dawn: the role of consistent song

425 transmission. *Ibis*, *145*(1), 120-129. https://doi.org/10.1046/J.1474-919X.2003.00130.X

426   Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of*

427   *Statistical Software*, 80(1), 1-28. doi:10.18637/jss.v080.i01

428

429   Bürkner, P.-C. and Charpentier, E. (2020). Modelling monotonic effects of ordinal predictors in

430   Bayesian regression models. *Br J Math Stat Psychol*, 73: 420-451.

431   https://doi.org/10.1111/bmsp.12195

432   Cardoso, G. C., & Price, T. D. (2010). Community convergence in bird song. *Evolutionary Ecology*, *24*,

433   447-461.

434   Dabelsteen, T., Larsen, O. N., & Pedersen, S. B. (1993). Habitat-induced degradation of sound

435   signals: Quantifying the effects of communication sounds and bird location on blur ratio, excess

436   attenuation, and signal-to-noise ratio in blackbird song. The Journal of the Acoustical Society of

437   America, 93(4), 2206-2220.

438

439   Darden, S. K., Pedersen, S. B., Larsen, O. N., & Dabelsteen, T. (2008). Sound transmission at ground

440   level in a short-grass prairie habitat and its implications for long-range communication in the swift

441   fox *Vulpes velox*. *The Journal of the Acoustical Society of America*, *124*(2), 758-766.

442   Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American*

443   *Naturalist*, *139*, S125-S153

444   Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in*

445   *medicine*, *27*(15), 2865-2873.

446   Grabarczyk, E. E., & Gill, S. A. (2020). Anthropogenic noise masking diminishes house wren

447   (*Troglodytes aedon*) song transmission in urban natural areas. *Bioacoustics*, *29*(5), 518-532.

448   Graham, B. A., Sandoval, L., Dabelsteen, T., & Mennill, D. J. (2017). A test of the Acoustic Adaptation

449   Hypothesis in three types of tropical forest: degradation of male and female Rufous-and-white

450   Wren songs. *Bioacoustics*, *26*(1), 37-61.

451

452   Hardt, B., & Benedict, L. (2020). Can you hear me now? A review of signal transmission and

453   experimental evidence for the acoustic adaptation hypothesis. *Bioacoustics*, *30*(6), 716-742.

454   https://doi.org/10.1080/09524622.2020.1858448

455

456   Holland, J., Dabelsteen, T., Pedersen, S. B., & Larsen, O. N. (1998). Degradation of wren *Troglodytes*

457   *troglodytes* song: implications for information transfer and ranging. *The Journal of the Acoustical*

458   *Society of America*, *103*(4), 2154-2166

459

460   Kime, N. M., Turner, W. R., & Ryan, M. J. (2000). The transmission of advertisement calls in Central

461   American frogs. *Behavioral Ecology*, *11*(1), 71-83

462

463   Lampe, H., Larsen, O., Pedersen, S., & Dabelsteen, T. (2007). Song degradation in the hole-nesting

464   pied flycatcher *Ficedula hypoleuca*: implications for polyterritorial behaviour in contrasting

465   habitat-types. *Behaviour*, *144*(10), 1161-1178.

466

467   LaZerte, S. E., Otter, K. A., & Slabbekoorn, H. (2015). Relative effects of ambient noise and habitat

468   openness on signal transfer for chickadee vocalizations in rural and urban green-spaces.

469   *Bioacoustics*, *24*(3), 233-252.

470   Leader, N., Wright, J., & Yom-Yov, Y. (2005). Acoustic properties of two urban song dialects in the

471   orange-tufted sunbird (Nectarinia osea). *The Auk*, *122*(1), 231-245.

472   Lohr, B., Wright, T. F., & Dooling, R. J. (2003). Detection and discrimination of natural calls in

473   masking noise by birds: estimating the active space of a signal. *Animal Behaviour*, *65*(4), 763-777.

474   Marten, K., & Marler, P. (1977). Sound transmission and its significance for animal vocalization - I.

475   Temperate habitats. *Behavioral Ecology and Sociobiology*, *2*(3), 271-290.

476   https://doi.org/10.1007/BF00299740

477   Morton, E. S. (1975). Ecological sources of selection on avian sounds. *The American Naturalist*,

478   109(965), 17-34.

479

480   Naguib, M., Schmidt, R., Sprau, P., Roth, T., Flörcke, C., & Amrhein, V. (2008). The ecology of vocal

481   signaling: male spacing and communication distance of different song traits in nightingales.

482   *Behavioral Ecology*, *19*(5), 1034-1040.

483   Nemeth, E., Dabelsteen, T., Pedersen, S. B., & Winkler, H. (2006). Rainforests as concert halls for

484   birds: Are reverberations improving sound transmission of long song elements? *The Journal of the*

485   *Acoustical Society of America*, *119*(1), 620. https://doi.org/10.1121/1.2139072

486

487   Pedersen, S. B. (1998). Preliminary operational manual for signal processor Sigpro. Centre of

488   Sound Communication, Odense University, Odense.

489

490   Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.

491   *Methods in Ecology and Evolution*, *1*(2), 103-113.

492

493   Tobias, J. A., Aben, J., Brumfield, R. T., Derryberry, E. P., Halfwerk, W., Slabbekoorn, H., & Seddon,

494   N. (2010). Song divergence by sensory drive in Amazonian birds. Evolution: *International Journal of*

495   *Organic Evolution*, *64*(10), 2820-2839. http://dx.doi.org/10.1111/j.1558-5646.2010.01067.x

496

497 Vargas-Castro, L. E., Sandoval, L., & Searcy, W. A. (2017). Eavesdropping avoidance and sound

498 propagation: the acoustic structure of soft song. *Animal behaviour*, *134*, 113-121.

499 Wheeldon A, Kwiatkowska K, Szymański P, Osiejuk TS (2022). Male and female song propagation in

500 a duetting tropical bird species in its preferred and secondary habitat. *PLoS ONE, 17*(10): e0275434.

501 https://doi.org/10.1371/journal.pone.0275434

502 Wiley, R. H., & Richards, D. G. (1978). Physical constraints on acoustic communication in the

503 atmosphere: implications for the evolution of animal vocalizations. *Behavioral ecology and*

504 *sociobiology*, *3*, 69-94

505 Yip, D. A., Bayne, E. M., Sólymos, P., Campbell, J., & Proppe, D. (2017). Sound attenuation in forest

506 and roadside environments: Implications for avian point-count surveys. *The Condor*, *119*(1), 73-84.

507 https://doi.org/10.1650/CONDOR-16-93.1