1

2

3   Aggression and multimodal signaling in noise in the European robin

4

5   Çağla Önsal[1], Alper Yelimlieş [1], Çağlar Akçay [1,2*]

6   [1] Department of Psychology, Koç University, İstanbul, Turkey

7   [2] School of Biological Sciences, Anglia Ruskin University, Cambridge, UK

8

9   ORCID

10   Çağla Önsal: **0000-0003-3131-6756**

11   Alper Yelimlieş: **0000-0003-2319-6141**

12   Çağlar Akçay: **0000-0003-0635-9586,**

13

14   **Corresponding author:**

15   Çağla Önsal

16   Department of Psychology

17   Koç University, İstanbul, Turkey

18   consal20@ku.edu.tr

19

20

21

22 Abstract

23 The effect on anthropogenic noise on acoustic signals is widely studied although the extent to

24 which this is due to short-term flexibility or long-term adaptation is unclear. Anthropogenic

25 noise may disrupt signals used to mediate aggressive interactions, leading to more physical

26 aggression between opponents. One solution to this problem is to switch signaling effort to a less

27 noisy modality (e.g. the visual modality). In the present study we ask whether urban and rural

28 European robins (*Erithacus rubecula*) use multi-modal signals flexibly in response to

29 anthropogenic noise during territorial defense. We predicted that during simulated intrusions

30 with experimental noise, European robins would increase their physical aggression, respond with

31 more visual threat displays and sing fewer songs, i.e. show a multi-modal shift. We also

32 predicted that urban birds, living in noisier habitats, would be generally more aggressive than

33 rural birds. The results showed that urban birds were more aggressive than rural robins, but an

34 increase in aggression with experimental noise was seen only in the rural birds. Urban birds also

35 used visual signals more often than rural birds. However, birds did not use visual signals more in

36 experimental noise. Instead, both urban and rural robins sang at higher rates under noise

37 conditions, thus increasing signaling effort in the noisy modality. These results point to a

38 complex role of immediate plasticity and longer-term processes in affecting communication

39 during aggressive interactions under anthropogenic noise.

40

41 Keywords:

43   Significance Statement

44   Human activity has an enormous effect on wildlife, including on their social behavior. Animals

45   living in urban areas often tend to be more aggressive than those living in rural areas, which may

46   be due to urban acoustic noise making communication between individuals more difficult. In a

47   study with a common songbird, the European robin, we investigated the role of urban acoustic

48   noise in aggression and territorial communication. Urban robins were more aggressive than rural

49   robins, and additional noise in the territory increased aggression in rural but not urban robins.

50   Robins increased their singing effort but did not increase visual signals in acoustic noise. These

51   results suggest that noise can indeed make animals behave more aggressively although the effect

52   may depend on how noisy it is already. These results further our understanding of how human-

53   made noise changes animal communication and social behavior.

54   Introduction

55   Urban habitats are polluted with anthropogenic noise, often in multiple modalities, which creates

56   challenges for urban-living wildlife (Brumm & Slabbekoorn, 2005). Many species rely heavily

57   on signals for communication in contexts such as mate attraction and territorial defense, and

58   noise from vehicles, buildings and other human activities often interferes with these signals

59   (Francis et al., 2009; Halfwerk & Slabbekoorn, 2015; Lee & Thornton, 2021). A well-studied

60   example of the effect of anthropogenic noise on communication is vocal signaling in urban birds:

61   in response to anthropogenic noise commonly found in cities, many species of birds may

62   increase repetition rates, amplitude or frequency characteristics of their acoustic signals (Brumm,

63   2004; Gil & Brumm, 2014; Slabbekoorn & den Boer-Visser, 2006; Wood & Yezerinac, 2006).

64   Urban living also leads to increased aggressiveness of individuals in urban habitats compared to

65   the rural habitats (Scales et al., 2011). The reasons for increased aggression in urban habitat are

66   not yet fully understood. It may result from several factors, including selection for bolder

67   individuals (Evans et al., 2010), increased food resources (Foltz et al., 2015), increased exposure

68   to harmful chemicals such as lead (McClelland et al., 2019) and less stable social environment

69   due to high rates of territory turnover in urban habitats (Davis et al., 2013). Anthropogenic noise

70   in urban habitats may also be responsible for increased aggression.

71   Animals often use signals in aggressive interactions (e.g. during territory defense) to resolve

72   conflicts with opponents. Use of signals is often beneficial for both parties if they can avoid

73   costly physical fights in this way (Maynard Smith & Price, 1973). Consequently, if signaling is

74   prevented or the signals are rendered ineffective, individuals may need to resort to higher levels

75   of physical aggression (Logue et al., 2010). Applied to urban habitats, this hypothesis suggests

76   that the high levels of urban noise may render long-distance aggressive signals less effective,

77   which in turn may lead to higher levels of aggression (Phillips & Derryberry, 2018). Consistent

78   with this hypothesis, some studies found a positive correlation between ambient noise levels and

79   aggressive behaviors (Akçay et al., 2020; Phillips & Derryberry, 2018; but see Kleist et al.,

80   2016).

81   Signalers employ various strategies to overcome interference from anthropogenic noise. We

82   focus here on the flexibility afforded by having signals in more than one modality (Bro-

83   Jørgensen, 2010; Halfwerk & Slabbekoorn, 2015; Partan & Marler, 1999). In such cases, animals

84   may shift their signals from the noisy modality to the less noisy modality to increase the

85   likelihood that the message of the signals gets through to the receivers (Partan et al., 2010;

86   Partan, 2017).

87   Few studies tested the multi-modal shift hypothesis in signals used in territorial interactions. In

88   one study, Ríos-Chelén et al. (2015) found that male red-winged blackbirds (*Agelaius*

89   *phoeniceus*) did not use more intense visual signaling in noisier territories although they

90   modified their acoustic signals. Another study on song sparrows (*Melospiza melodia*) found that

91   males in noisier urban habitats were both more aggressive and used proportionally more visual

92   threat signals (wing waves) during territory defense compared to the males in rural habitats,

93   consistent with a multi-modal shift (Akçay et al., 2019). In another experiment, however,

94   individual song sparrows did not increase their visual signaling effort when experimentally

95   presented with noise, suggesting that multi-modal shift was not due to immediate plasticity

96   (Akçay & Beecher, 2019).

97   Here we investigate the responses of European robins (*Erithacus rubecula*) living in urban and

98   rural habitats in Istanbul, Turkey, to simulated territorial intrusions with or without experimental

99   noise playback. European robins have both visual and acoustic signals that are used in agonistic

100   interactions (Lack, 1965). Previous studies have found that robins respond both to song and

101   visual signals during territorial intrusions (Chantrey & Workman, 1984). Territory holders sing

102   in response to the song of an intruder, while visual signals are used when the intruding male is

103   within range of vision. Their most prominent visual signal is the neck display, which has been

104   observed in response to the sight of a rival male's red neck, or indeed even a ball of red feathers

105   (Lack, 1965). Other visual territorial defense signals include wing flutters, pricking the tail up,

106   and swaying, where the resident male moves his head from one side to the other (Lack, 1965).

107   There have been several studies on the singing and aggressive behaviors of robins in the

108   presence of noise. A study by Mclaughlin and Kunc (2013) found that robins, after being lured

109   by playback of a robin song from a speaker, tended to move away from the speaker when the

110   speaker switched to playback of low-frequency noise mimicking typical traffic noise, particularly

111   when the amplitude of noise was high (90 dB at 1m). In response increasing amplitude of noise,

112   the robins sang shorter songs with fewer notes and increased the minimum frequency of their

113   songs. In another study, experimental presentation of wind turbine noise during simulated

114   territorial intrusions led to a decrease in low frequency elements in the songs, at the same time

115   leading to an increase in flight rates (Zwart et al., 2016). Song rates did not significantly differ

116   between the noise and no-noise conditions. Interestingly, fewer robins used visual threat postures

117   under experimental presentation of noise compared to no noise, although the difference was not

118   significant (Zwart et al. 2016).

119   The presence of both acoustic and visual signals in territorial defense makes the European robin

120   a suitable candidate for testing the multimodal shift hypothesis but to our knowledge no previous

121   study compared visual signaling between urban and rural robins. We predict that robins in urban

122   habitats will exhibit higher levels of visual signaling. Additionally, if such a multi-modal shift is

123   due to phenotypic plasticity, robins should increase their visual signaling under experimental

124   noise. Finally, in accordance with earlier studies, we also expect to see a greater level of

125   aggression from urban robins compared to rural robins. If increased aggression is due to

126   individual plasticity in response to noise, we also expect higher levels of aggression from robins

127   in response to experimental noise.

128   Methods

129   *Study site*s and species

130   We carried out playback experiments with male European robins that held territories in rural

131   areas (forests around Sarıyer, Istanbul, 41° 9' 50.73971"N, 29° 0' 32.25243"E) and urban parks

132   and green areas in Sarıyer, Istanbul, Turkey in April and May 2021 (urban: n=9; rural: n=12).

133   Robin territories were detected by the presence of an already-singing male robin before the first

134   playback or during recording sessions prior to playback. We determined a central location by

135   observing the robin's flights for about 5 minutes, although we did not attempt to map the entire

136   territory. In all trials reported below, only a single bird responded to the playback (in one case,

137   we aborted the trial when a second male came to within 10 m of the speaker). It was not possible

138   to record data blind as our study involved observing focal individuals in the field and noise

139   manipulation was audible to all observers.

140   *Stimuli*

141   Playback stimuli were generated on the software Syrinx (John Burt, Portland, OR) from male

142   European robin songs recorded in March 2021 in four of the nine study sites. We generated

143   stimuli tapes by extracting high quality songs from each recording and filtering out low

144   frequency noise below 1000 Hz. We added a silent period after each song so that stimuli were

145   presented at a rate of one song per seven seconds. The songs lasted on average (±SD) 2.36

146   (±0.49). We created one-minute stimuli (consisting of nine different songs) which were repeated

147   three times to make up three-minute stimuli to be played during the trials. In total, we used 17

148   tapes created from the songs of 17 different robins. The stimulus played for each subject came

149   from a robin whose territory was separated by at least one km from that of the subject's territory.

150   Each subject received the same stimulus in both trials.

151   We generated the experimental acoustic noise stimuli by filtering white noise (created with

152   Audacity) with the average amplitude spectrum from a 1-minute recording (made with a Marantz

153   PMD660 and ME66/K6 microphone) of traffic noise in Sarıyer, Istanbul using the package

154   *seewave* in R (Sueur et al., 2008).

155   As a visual stimulus, we used a 3-D printed bird model (dimensions, height: 8 cm, length: 12 cm,

156   width: 4.5 cm) which was hand-painted to resemble an adult robin.

157   *Experimental procedure and design*

158   We started each trial by locating a European robin territory and observing the singing posts for

159   about ~5m. We then placed the robin model attached to a speaker (Anker Soundcore Bluetooth

160   Speaker, Anker, Inc.) on a natural perch at the estimated center of the resident male's territory,

161   approximately 1.5 m above the ground. A second Bluetooth speaker (same model as above) was

162   placed on the ground, face-up below the first, for noise playback. In the control condition, the

163   second speaker was placed but not turned on, so the resident male received only song playback.

164   In the noise condition, in addition to the song playback, traffic noise was played at 75 dB SPL at

165   1 m. The noise playback lasted for the entire duration of the song playback.

166 Each subject received two 3-minute trials, one with experimental noise and one without noise.

167 The order of the conditions was counterbalanced, and the two trials were separated with a break

168 period that lasted for approximately an hour. Two observers, about 10 m away from the

169 experimental setup, recorded the songs and calls of the resident robin. The observers also

170 narrated the trials, noting flights (any airborne movement by the bird), distance with each flight,

171 and visual displays described in Table 1. We continued recording songs for 3 minutes after the

172 end of each trial. Recordings were made on a Marantz PMD660 with a Sennheiser ME66/K6

173 microphone, or on a Zoom H5 handheld recorder with a Zoom SGH6 shotgun microphone.

174 In 31 of the trials, the bird was already singing when we started the trial. For these birds, the 3-

175 minute playback period started with the first song played. In 11 of the trials, where the subject

176 was quiet when the playback started, the 3-minute playback period started with their first

177 response (song or approach). The average duration of pretrial playback for these 11 trials was

178 64.9 seconds (SD = 40.8).

179 After each trial, we measured the ambient noise with a VLIKE VL6708 sound-level meter with

180 the method described in (Brumm, 2004). We took eight measurements (two in each cardinal

181 direction) within a minute period, which were then averaged. Noise levels were highly repeatable

182 across trials (intra-class coefficient, r=0.96, p<0.00001; for three subjects, we only had noise

183 measurements from a single trial).

184 *Response variables and data analysis*

185 We scanned recordings using the Syrinx software (John Burt, Portland, OR). All analysis was

186 carried out in R. The number of songs and visual displays (neck displays, swaying, wing flutters)

187 were extracted form sonograms created on Syrinx. We only analyzed song rates and durations, as

188   overlapping stimulus and subject songs made it impossible to determine with certainty the note

189   compositions for most songs. We also extracted from recordings the number of flights, closest

190   approach to the model/speaker and proportion of time spent within 5m of the speaker. The latter

191   three spatial variables were taken as aggressive behaviors. Because these variables were

192   significantly correlated with each other, we carried out a principal component analysis (PCA)

193   using the *principal* function in package *psych* (Revelle, 2021). The first component of PCA

194   (PCA1) explained 61% of variance and was taken as our primary measure of aggression (see

195   Table 2 for loading coefficients). Since only 8 subjects used any visual displays during the

196   experimental period, we coded this variable as a binomial variable (visual signal present vs.

197   absent).

198   We first checked whether urban territories had higher ambient noise with a linear mixed model

199   (LMM) using habitat type (urban vs. rural) as the predictor variable and territory ID as the

200   random variable. We also assessed whether noise levels were repeatable using the *rptR* package

201   (Stoffel et al., 2017).

202   We then checked whether order of trials had a significant effect on aggression scores, song rates

203   and visual signaling. The order of trials did not have a significant effect on song rate (LMM,

204   coefficient = 0.51, SE = 0.78, p = 0.52) or aggression score (LMM, coefficient = -0.22, SE =

205   0.15, p = 0.16). However, there was a significant order effect on the incidence of visual displays

206   (GLMM, estimate = -15.32, SE = 6.22, p = 0.01). Eight subjects used visual displays in the first

207   trial, compared to two in the second trial (both of these subjects also used visual displays in the

208   first trial). Because of this order effect, we only used the first trial for each subject when

209   analyzing the presence or absence of visual displays.

210

211   We analyzed song rates and aggression scores with linear mixed models (LMM), using the *lme*

212   fuction in the package *nlme* (Pinheiro et al., 2022). We took habitat type (urban vs. rural) and

213   experimental condition (noise vs. control) as the predictor variables, and male ID as the random

214   variable. We applied a generalized linear model (with log-link, using the "*glm*" function in base

215   R) with visual displays as binomial response variable, and habitat and condition as predictor

216   variables, using only the first trials for each subject. Since only two rural subjects used visual

217   displays, we also carried out this analysis with the subset of only urban birds (see Supplementary

218   Materials).

219   Results

220   Urban habitats had significantly higher levels of ambient noise than rural habitats (urban: M =

221   49.0, SD = 7.1; rural: M = 39.9, SD = 3.6) and noise measurements were highly repeatable

222   between the two trials (intra-class correlation coefficient; r=0.96, standard error: 0.02; p <

223   0.0001).

224   Urban birds were significantly more aggressive than rural birds. There was no main effect of

225   condition but there was a significant interaction effect of habitat and condition. To understand

226   this interaction effect, we carried out separate LMMs with rural and urban birds with condition

227   as predictor variable and territory ID as random variable. Rural birds were more aggressive

228   under the experimental noise condition, whereas there was no effect of experimental noise on

229   aggression in urban birds (Table 3).

230   Song rates did not differ significantly between urban and rural birds. Both urban and rural birds

231   sang at higher rates under experimental noise. The interaction effect of habitat and experimental

232   condition was not significant (Table 3). There was no effect of habitat and condition on song

233   length (see Table 3).

234   Urban birds used visual threat displays in the first trials significantly more than their rural

235   counterparts (GLM; χ^2= 9.75, p=0.0018; Figure 2). Experimental noise did not have a significant

236   effect on the use of visual signals, although more birds (5 out of 5) used visual threat displays in

237   no noise condition than in noise condition (1 out of 4 birds; χ^2= 3.22, p=0.07).

238   Discussion

239   The present study was designed to examine the role of noise in determining aggressiveness and

240   aggressive signaling. We had predicted that urban robins, living in noisier territories will be more

241   aggressive compared to rural robins in simulated territorial intrusions and experimental noise

242   during simulated intrusions will change both their aggressive behaviors and signaling behaviors.

243   Particularly, we expected that experimental acoustic noise should increase aggression during

244   intrusions and lead to an increase in using signals in the visual modality. In line with our first

245   prediction, we found that urban robins responded with significantly more aggressive behaviors

246   (approach and flights) to simulated intrusions than rural robins. The effect of experimental noise

247   on aggressive approach was dependent on the habitat: while experimental noise led to increased

248   aggression in the (comparatively quiet) rural habitats, it had no effect in the noisy urban habitats.

249   In both habitat types, experimental noise led to an increase in song rates, but no change was

250   observed in song duration or the presence of visual signals which tended to be less common

251   under experimental noise in the urban habitats.

252   *Noise and aggressive behaviors in territory defense*

253   Our results on the effect of habitat on aggression replicates earlier findings that urban-living

254   birds are more aggressive than rural birds (Evans et al. 2010, Davies and Sewall, 2016, Phillips

255   and Derryberry, 2018). We also extend previous findings by showing that the effect of

256   experimental noise on aggression was dependent on habitat: urban males showed no further

257   increases in aggression with experimental noise while rural males showed a significant increase

258   in aggression. The increased aggression with experimental noise in rural habitats is consistent

259   with the idea that urban noise has a causal role in increasing aggression. In contrast, for urban

260   males that are already living in noisy territories, additional noise may not have as much as an

261   effect as in rural habitats. Urban birds may also be more habituated to acute sources of noise (e.g.

262   a car passing or idling next to their territory) than rural birds, although they did show a plastic

263   response in their singing rate. Finally, urban birds may not be able to increase their already high

264   levels of aggression in response to noise playback.

265   Only a small number of studies experimentally manipulated noise levels to examine a causal role

266   of noise in increased aggression. These studies yielded mixed results. Grabarcyzk and Gill

267   (2019) found that house wrens (*Troglodytes aedon*) males attacked the simulated intruder more

268   frequently when playback was accompanied with experimental noise than when it wasn't,

269   consistent with the hypothesis that noise induces higher levels of aggression. Another study in

270   song sparrows however, found no effect of experimental noise on aggression levels, measured as

271   time spent within one meter of the speaker, or attacks (Akçay & Beecher, 2019). It is worth

272   noting that in the latter study, the noise playback in that study started only when subjects

273   approached to within five meters, which all subjects did within a short period of time (< 1

274   minute). Thus, lack of an effect in physical proximity may be due the fact that subjects already

275   were close to the speaker when the noise playback started.

276   In another study, Zwart et al. (2016) found that European robins did not show a statistically

277   significant increase in aggressive behaviors in response to experimental wind turbine noise

278   during simulated intrusions, although some variables like flights did show a trend consistent with

279   higher aggression with experimental noise. Given the fact that this study had a between-subject

280   design and a relatively small sample size per treatment group (8 birds) the non-significant

281   differences may be primarily due to lack of power rather than lack of an effect. Finally, a recent

282   study by Reed et al (2021) in lazuli buntings (*Passerina amoena*) and spotted towhees (*Pipilo*

283   *maculatus*) found that experimental presentation of natural noise (such as noise from a river,

284   ocean surf or cicadas) at the landscape level led to slower detection of a simulated intruder and

285   consequently weaker approach responses (see also Kleist et al. 2016).

286   Together these studies point to two apparently contradictory effects of noise on territorial

287   aggression. On one hand, noise may make localization of the simulated intruder and perception

288   of stimulus features more difficult, leading to slower or weaker approach behaviors (Kleist et al.

289   2016; Reed et al. 2012; Templeton et al. 2016). On the other hand, assuming the simulated

290   intruder is located, noise may interfere with the signaling behaviors of subjects which may

291   induce them to resort to higher physical aggression (e.g. Grabarcyzk and Gill, 2019). The

292   differences in the findings may be due in part to differences experimental designs, particulary

293   with respect to the presentation of the noise stimulus (e.g. type of noise, location of noise relative

294   to the conspecific stimulus etc.). Therefore, to investigate the causal effect of noise on territorial

295   aggression, it would be useful to have a more approach systematic approach to varying noise

296   stimulus presentation.

297   *Change in multi-modal signals with noise*

298   We also found that European robins changed their signaling behaviors in response to noise. In

299   the acoustic modality, robins increased their song rate in both habitat types, without changing

300   song length. Increasing song rate may mean that the robins are attempting to increase the serial

301   redundancy of their signals, as has been found for chaffinches (*Fringella coelebs*) in a study by

302   Brumm and Slater (2006). It is worth noting however that the chaffinches sing with eventual

303   variety, repeating the same song type multiple times before switching to a new song type. Thus,

304   the finding in Brumm and Slater that the males sang longer bouts of the same song type in

305   noisier habitats amounts to increasing serial redundancy. Robins, in contrast, are immediate

306   variety singers, switching song types with each song. Whether increasing song rate also increases

307   serial redundancy of the signal is therefore unclear and depends on whether the song types are

308   largely interchangeable.

309   Other studies looking at the effect of noise on singing rate found mixed results. A study on red-

310   winged blackbirds had previously found lower song rate in response to noise (Ríos-Chelén et al.,

311   2015), while a more recent study in chaffinches found no difference in song rates between urban

312   and rural birds. In studies that simulated territorial intrusions with or without experimental noise,

313   the results were also mixed: experimental noise did not lead to changes in song rate in house

314   wrens or song sparrows during a simulated intrusion (Akçay & Beecher, 2019; Grabarczyk &

315   Gill, 2019).

316   One of our main research questions was whether robins would switch to preferentially signaling

317   in the visual modality in response to acoustic noise. We found that urban birds were more likely

318   to use visual signals than rural birds, with six out of nine urban birds using visual threat displays

319   compared with two out of 12 rural birds. We did not, however, detect a shift from the acoustic

320   signals to the visual signals under experimental noise. One caveat to this conclusion is the fact

321   that most visual displaying was confined to the first trials which prevented us from testing the

322   individual phenotypic plasticity. Nevertheless, limiting our analysis to the first trials only, we

323   found that visual displays were more prevalent without the experimental noise than with it, albeit

324   the difference did not reach significance. This finding is similar to that of Zwart et al (2016),

325   where slightly lower rates of visual signaling were observed in noise. Thus, while increased

326   visual signaling in urban birds is compatible for a multi-modal shift, such a multi-modal shift

327   doesn't seem to be due to the plastic responses to acoustic noise.

328   These findings are similar to the earlier studies in song sparrows. Like in the robins, urban song

329   sparrows use proportionally more wing waves (a visual threat signal) as part of their aggressive

330   signaling during a simulated intrusion, compatible with a multi-modal shift (Akçay et al., 2019).

331   The multi-modal shift, however, does not appear to be due to individual phenotypic plasticity, as

332   song sparrows did not increase their visual signaling effort during experimental presentation of

333   acoustic noise (Akçay & Beecher, 2019). Thus, an increase in visual signaling may be due to

334   either long-term selection for different signaling strategies or plasticity due the chronic (rather

335   than acute) effect of noise. These hypotheses need to be tested with further studies, ideally with

336   marked individuals that can be followed for extended periods of time during exposure to chronic

337   noise.

338   *Conclusion*

339   In summary, we found that urban European robins were more aggressive than rural ones and the

340   effect of noise on the change in aggressive behaviors depended on the habitat: while urban birds

341   did not behave more aggressively, rural birds did so under experimental presentation of noise.

342   Both urban and rural birds increased their song rate (but not song length) under experimental

343   noise and urban birds used visual threat displays more frequently than rural birds. These findings

344   extend previous studies on the change in aggressive behaviors and signaling with noise. Going

345   forward experimental analyses of the effect of noise in signaling and aggressive behaviors will

346   prove valuable in determining the role of plasticity in how urban-living species adapt to life in a

347   noisy world.

348   Disclosure of potential conflicts of interest

349   The authors declare that they have no conflicts of interest.

350   Research involving Human Participants and/or Animals

351   All procedures used in this study follow the ASAB/ABS guidelines for the treatment of animals

352   in behavioral research and teaching. Subjects were not captured or handled before, during or

353   after any of the trials. Time spent within a territory did not exceed 15 minutes per trial, and 30

354   minutes per day.

355   Informed consent

356   The research did not involve human participants.

357   Data availability statement

358   The raw data and the R-code to reproduce the analyses reported in the manuscript is available as

359   a supplementary material and will be deposited at a public repository before the manuscript is

360   published.

361   Acknowledgements

364   References

365   Akçay, Ç., Beck, M. L., & Sewall, K. B. (2019). Are signals of aggressive intent less honest in

366   urban habitats? *Behavioral Ecology*, arz179. https://doi.org/10.1093/beheco/arz179

367   Akçay, Ç., & Beecher, M. D. (2019). Multi-modal communication: Song sparrows increase

368   signal redundancy in noise. *Biology Letters*, *15*(10), 20190513.

369   https://doi.org/10.1098/rsbl.2019.0513

370   Akçay, Ç., Porsuk, Y. K., Avşar, A., Çabuk, D., & Bilgin, C. C. (2020). Song overlapping, noise,

371   and territorial aggression in great tits. *Behavioral Ecology*, *31*(3), 807–814.

372   https://doi.org/10.1093/beheco/araa030

373   Bro-Jørgensen, J. (2010). Dynamics of multiple signalling systems: Animal communication in a

374   world in flux. *Trends in Ecology & Evolution*, *25*(5), 292–300.

375   https://doi.org/10.1016/j.tree.2009.11.003

376   Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird.

377   *Journal of Animal Ecology*, *73*(3), 434–440. https://doi.org/10.1111/j.0021-

378   8790.2004.00814.x

379   Brumm, H., & Slabbekoorn, H. (2005). Acoustic Communication in Noise. In *Advances in the*

380   *Study of Behavior* (Vol. 35, pp. 151–209). Academic Press.

381   https://doi.org/10.1016/S0065-3454(05)35004-2

382   Mclaughlin, K., & Kunc, H. (2013). Experimentally increased noise levels change spatial and

383   singing behaviour. *Biology Letters*, *9*. https://doi.org/10.1098/rsbl.2012.0771

384   Chantrey, D. F & Workman L. (1984). Song and plumage effects on aggressive display by the

385   European Robin (Erithacus rubecula). *Ibis*, *126*, 366-371.

386   Davis, A., Major, R. E., & Taylor, C. E. (2013). Housing Shortages in Urban Regions:

387   Aggressive Interactions at Tree Hollows in Forest Remnants. *PLoS ONE*, *8*(3), e59332.

388   https://doi.org/10.1371/journal.pone.0059332

389   Davies, S., & Sewall, K. B. (2016). Agonistic urban birds: elevated territorial aggression of

390   urban song sparrows is individually consistent within a breeding period. *Biology letters*,

391   *12*(6), 20160315.

392   Deoniziak, K., & Osiejuk, T. S. (2016). Disentangling relations among repertoire size, song

393   rate, signal redundancy and ambient noise level in European songbird. *Ethology*, *122*(9),

394   734-744.

395   Evans, J., Boudreau, K., & Hyman, J. (2010). Behavioural Syndromes in Urban and Rural

396   Populations of Song Sparrows. *Ethology*. https://doi.org/10.1111/j.1439-

397   0310.2010.01771.x

398   Foltz, S. L., Ross, A. E., Laing, B. T., Rock, R. P., Battle, K. E., & Moore, I. T. (2015). Get off

399   my lawn: Increased aggression in urban song sparrows is related to resource availability.

400   *Behavioral Ecology*, *26*(6), 1548–1557. https://doi.org/10.1093/beheco/arv111

401   Francis, C. D., Ortega, C. P., & Cruz, A. (2009). Noise Pollution Changes Avian Communities

402   and Species Interactions. *Current Biology*, *19*(16), 1415–1419.

403   https://doi.org/10.1016/j.cub.2009.06.052

404   Gil, D., & Brumm, H. (2014). Acoustic communication in the urban environment: Patterns,

405   mechanisms, and potential consequences of avian song adjustments. In *Avian Urban*

406   *Ecology*. Oxford University Press.

407   https://doi.org/10.1093/acprof:osobl/9780199661572.003.0006

408   Grabarczyk, E. E., & Gill, S. A. (2019). Anthropogenic noise affects male house wren response

409   to but not detection of territorial intruders. *PLOS ONE*, *14*(7), e0220576.

410   https://doi.org/10.1371/journal.pone.0220576

411   Halfwerk, W., & Slabbekoorn, H. (2015). Pollution going multimodal: The complex impact of

412   the human-altered sensory environment on animal perception and performance. *Biology*

413   *Letters*, *11*(4), 20141051. https://doi.org/10.1098/rsbl.2014.1051

414   Kleist, N. J., Guralnick, R. P., Cruz, A., & Francis, C. D. (2016). Anthropogenic noise weakens

415   territorial response to intruder's songs. *Ecosphere*, *7*(3), e01259.

416   Lack, D. (1943). The life of the Robin. (1st ed.). London, Witherby.

417   Lee, V. E., & Thornton, A. (2021). Animal Cognition in an Urbanised World. *Frontiers in*

418   *Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.633947

419   Logue, D. M., Abiola, I. O., Rains, D., Bailey, N. W., Zuk, M., & Cade, W. H. (2010). Does

420   signalling mitigate the cost of agonistic interactions? A test in a cricket that has lost its

421   song. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1693), 2571–2575.

422   https://doi.org/10.1098/rspb.2010.0421

423   Maynard Smith, J., & Price, G. (1973). The Logic of Animal Conflict. *Nature*. *246, 15-18*

424   https://doi.org/10.1038/246015A0

425   McClelland, S. C., Durães Ribeiro, R., Mielke, H. W., Finkelstein, M. E., Gonzales, C. R., Jones,

426   J. A., Komdeur, J., Derryberry, E., Saltzberg, E. B., & Karubian, J. (2019). Sub-lethal

427   exposure to lead is associated with heightened aggression in an urban songbird. *Science*

428   *of The Total Environment*, *654*, 593–603. https://doi.org/10.1016/j.scitotenv.2018.11.145

429   Mclaughlin, K., & Kunc, H. (2013). Experimentally increased noise levels change spatial and

430   singing behaviour. *Biology Letters, 9*. https://doi.org/10.1098/rsbl.2012.0771

431   Partan, S. R., & Marler, P. (1999). Communication goes multimodal. *Science (New York, N.Y.)*,

432   *283*(5406), 1272–1273. https://doi.org/10.1126/science.283.5406.1272

433   Partan, S. R., Fulmer, A. G., Gounard, M. A., & Redmond, J. E. (2010). Multimodal Alarm

434   Behavior in urban and rural gray squirrels studied by means of observation and a

435   mechanical robot. *Current Zoology*, *56*(3), 313–326.

436   https://doi.org/10.1093/czoolo/56.3.313

437   Partan, S. R. (2017). Multimodal shifts in noise: Switching channels to communicate through

438   rapid environmental change. *Animal Behaviour*, *124*, 325–337.

439   https://doi.org/10.1016/j.anbehav.2016.08.003

440   Phillips, J. N., & Derryberry, E. P. (2018). Urban sparrows respond to a sexually selected trait

441   with increased aggression in noise. *Scientific Reports*, *8*(1), 7505.

442   https://doi.org/10.1038/s41598-018-25834-6

443   Pinheiro J, Bates D, R Core Team (2022). *nlme: Linear and Nonlinear Mixed Effects Models*. R

444   package version 3.1-157, https://CRAN.R-project.org/package=nlme.

445   Revelle, W. (2021). *psych: Procedures for Psychological, Psychometric, and Personality*

446   *Research* (2.1.9). https://CRAN.R-project.org/package=psych

447   Reed, V. A., Toth, C. A., Wardle, R. N., Gomes, D. G. E, Barber, J. R., Francis, C. D., Natural

448   noise affects conspecific signal detection and territorial defense behaviors in songbirds,

449   *Behavioral Ecology*, Volume 32, Issue 5, September/October 2021, Pages 993–1003

450   Ríos-Chelén, A. A., Lee, G. C., & Patricelli, G. L. (2015). Anthropogenic noise is associated

451   with changes in acoustic but not visual signals in red-winged blackbirds. *Behavioral*

452   *Ecology and Sociobiology*, *69*(7), 1139–1151. https://doi.org/10.1007/s00265-015-1928-7

453   Scales, J., Hyman, J., & Hughes, M. (2011). Behavioral Syndromes Break Down in Urban Song

454   Sparrow Populations: Behavioral Syndromes Break Down in Urban Song Sparrow

455   Populations. *Ethology*, *117*(10), 887–895. https://doi.org/10.1111/j.1439-

456   0310.2011.01943.x

457   Slabbekoorn, H., & den Boer-Visser, A. (2006). Cities Change the Songs of Birds. *Current*

458   *Biology*, *16*(23), 2326–2331. https://doi.org/10.1016/j.cub.2006.10.008

459   Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and

460   variance decomposition by generalized linear mixed-effects models. *Methods in Ecology*

461   *and Evolution*, *8*(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797

462   Sueur, J., Aubin, T., & Simonis, C. (2008). Seewave, a Free Modular Tool for Sound Analysis

463   and Synthesis. *Bioacoustics*, *18*(2), 213–226.

464   https://doi.org/10.1080/09524622.2008.9753600

465   Templeton, C. N., Zollinger, S. A., & Brumm, H. (2016). Traffic noise drowns out great tit alarm

466   calls. *Current Biology*, *26*(22), R1173-R1174.

467   Wolfenden, A. D., Slabbekoorn, H., Kluk, K., & Kort, S. R. (2019). Aircraft sound exposure

468   leads to song frequency decline and elevated aggression in wild chiffchaffs. *Journal of*

469   *Animal Ecology*, *88*(11), 1720–1731. https://doi.org/10.1111/1365-2656.13059

470   Wood, W. E., & Yezerinac, S. M. (2006). Song Sparrow (Melospiza Melodia) Song Varies with

471   Urban Noise. *The Auk*, *123*(3), 650–659. https://doi.org/10.1093/auk/123.3.650

472   Zwart, M. C., Dunn, J. C., McGowan, P. J. K., & Whittingham, M. J. (2016). Wind farm noise

473   suppresses territorial defense behavior in a songbird. *Behavioral Ecology*, *27*(1), 101–

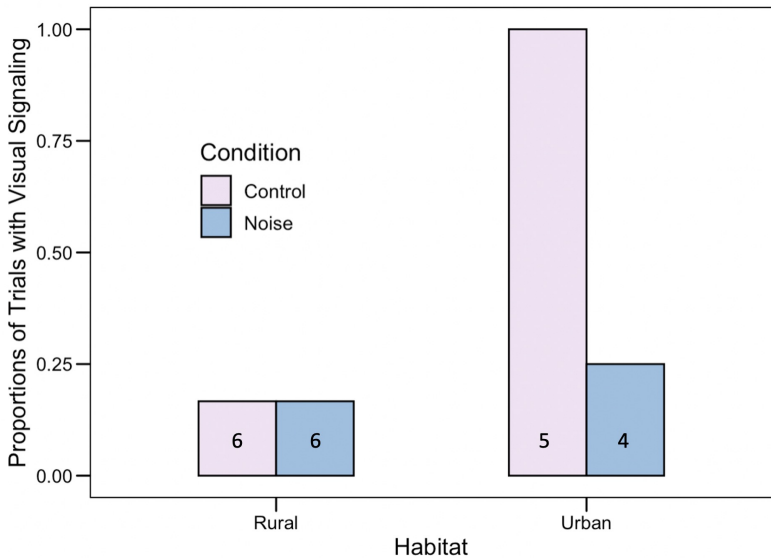474   108. https://doi.org/10.1093/beheco/arv128

475

A

B
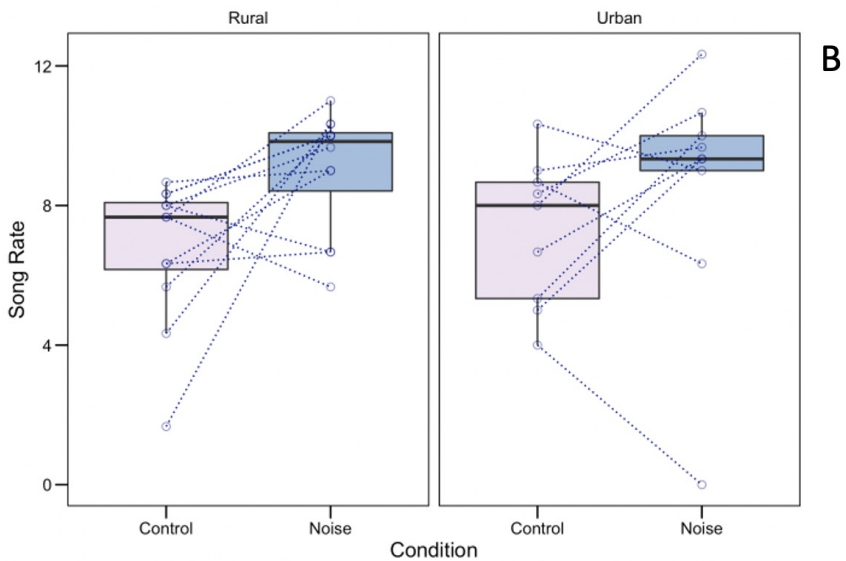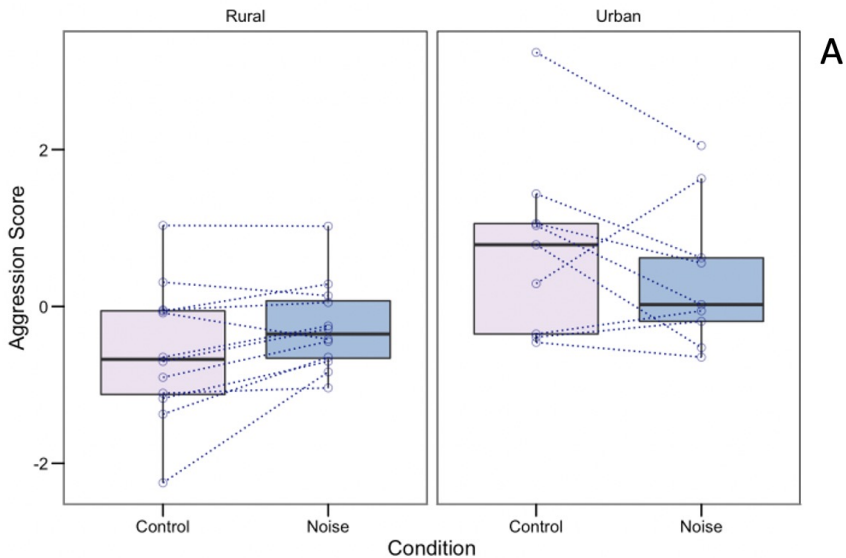
Figure 1. The relationship of aggression scores (A) and song rate (B) with habitat and condition. The boxes indicate interquartile ranges, the middle line indicates median, and whiskers indicate 95% confidence intervals. Dot connected by dotted lines represent data from individual subjects.

Figure 2. Proportions of first trials where the resident male used visual signals, grouped by habitat and treatment condition. The numbers at the bottom of each bar indicates the total number of subjects for each combination.

Table 1. Visual displays of European robins during territorial interactions

Behavior	Description
Neck display	The robin raises his head, displaying his neck.
Wing flutter	The robin flutters his wings.
Swaying	The robin rhythmically sways his body from one side to the other.
Tail up	The robin perks his tail up.

Table 2. Loading coefficients of the Principal Component Analysis.

Factor	Loading coefficient to PC1
Flight rate	0.65
Proportion of time spent within 5 meters	0.83
Closest approach distance	-0.85
SS loadings	1.83
%Variance	61%

Table 3. Coefficients (SE) from the linear mixed models and the p-values from Wald t tests, examining the effect of habitat and experimental noise treatment. Statistically significant values are shown in bold type

	Aggression Score		Song Rate		Song Length	
Predictors	*Estimates (SE)*	*p*	*Estimates (SE)*	*p*	*Estimates (SE)*	*p*
(Intercept)	-0.58 (0.26)	**0.035**	6.75 (0.69)	**<0.001**	1.81(0.15)	**<0.001**
Condition	1.32 (0.39)	**0.003**	0.51(1.05)	0.635	0.07(0.23)	0.744
Habitat	0.32 (0.19)	0.105	2.28 (0.89)	**0.019**	0.07(0.11)	0.565
Condition*Habitat	-0.68 (0.29)	**0.031**	-1.02 (1.36)	0.464	0.07(0.18)	0.679