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Anthropogenic noise affects vocal interactions

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1 **Title: Anthropogenic noise affects vocal interactions**

2 **Short title for page headings: Noise affects vocal interactions**

3

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16

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21

22

23 **Abstract**

24 Animal communication plays a crucial role in many species, and it involves a sender
25 producing a signal and a receiver responding to that signal. The shape of a signal is
26 determined by selection pressures acting upon it. One factor that exerts selection on
27 acoustic signals is the acoustic environment through which the signal is transmitted.
28 Recent experimental studies clearly show that senders adjust their signals in response to
29 increased levels of anthropogenic noise. However, to understand how noise affects the
30 whole process of communication, it is vital to know how noise affects the receiver's
31 response during vocal interactions. Therefore, we experimentally manipulated ambient
32 noise levels to expose male European robins (*Erithacus rubecula*) to two playback
33 treatments consisting of the same song: one with noise and another one without noise. We
34 found that males responding to a conspecific in a noise polluted environment increased
35 minimum frequency and decreased song complexity and song duration. Thus, we show
36 that the whole process of communication is affected by noise, not just the behaviour of
37 the sender.

38

39 **1. Introduction**

40 Communication plays a crucial role in many species as it is used in sexual selection
41 through both female choice and male-male competition, in parental care among parents
42 and their offspring, and in predator prey interaction (Bradbury and Vehrencamp, 2011).
43 Animal communication in its simplest form involves a sender producing a signal that
44 conveys information, and a receiver making a decision on how to respond to that signal
45 (Bradbury and Vehrencamp, 2011). During such vocal interactions individuals exchange
46 information about their quality, status or motivation (Todt and Naguib, 2000;
47 Vehrencamp, 2000). Thus, for the process of communication to be completed, it is vital
48 that the sender is able to successfully transmit the signal across the environment to the
49 receiver.

50

51 The shape of a signal is determined by different constraints. Sexually selected
52 traits, such as bird song, are shaped by an interaction between sexual selection and other
53 natural selection pressures. Sexual selection favours the elaboration of traits, whereas the
54 elaboration of a trait might be counteracted by natural selection processes optimizing
55 both transmission and detectability of signals (e.g. Wiley and Richards, 1982; Patricelli
56 and Blickley, 2006). One environmental factor that exerts selection pressure on acoustic
57 signals is ambient noise, which can mask the information in a signal (Ryan and
58 Brenowitz, 1985). A relatively novel form of ambient noise is anthropogenic noise.

59

60 A growing number of experimental studies have demonstrated that senders adjust
61 their signals to anthropogenic noise. In birds, one strategy to avoid masking of signals by

62 low-frequency anthropogenic noise is through an increase in minimum frequency
63 (Halfwerk and Slabbekoorn, 2009; Gross et al., 2010; Verzijden et al., 2010; Bermudez-
64 Cuamatzin et al., 2011; Hanna et al., 2011; McLaughlin and Kunc, 2013; Montague et al.,
65 2013). A similar response to increasing noise levels was reported in anura where
66 individuals called at higher dominant frequencies when experimentally exposed to
67 anthropogenic noise (Cunnington and Fahrig, 2010). Thus, increasing anthropogenic
68 noise levels have a clear impact on the signalling behaviour of the sender. These changes
69 in signal characteristics also affect the response of receivers. Great tits, for example,
70 respond differently to conspecific songs recorded in noisy areas than in quiet areas when
71 background noise was removed (Mockford and Marshall, 2009). However, to understand
72 how noise affects the whole process of communication, it is vital to know how noise
73 affects song during vocal interactions.

74

75 In the European robin, *Erithacus rubecula*, males produce complex songs, and
76 they use their song to interact with conspecifics (Hoelzel, 1986; Brindley, 1991). Recent
77 studies showed that robins also adjust their songs to increasing noise levels. Robins
78 recorded in noisy locations sang songs at higher minimum frequencies, which were less
79 complex and shorter in duration as songs recorded in quiet locations. These observational
80 findings were then confirmed by noise exposer experiments (McLaughlin and Kunc,
81 2013; Montague et al., 2013). Thus, robins provide an ideal model to test also how
82 individuals during a vocal interaction are affected by anthropogenic noise.

83

84 The aim of this study was to investigate how noise affects responses during vocal
85 interactions. We experimentally manipulated ambient noise levels to expose male
86 European robins (*Erithacus rubecula*) to two playback treatments consisting of the same
87 song: one with noise and another one without noise (Fig. 1). If vocal interactions were
88 affected by changes in noise during the playbacks we predicted a different response to the
89 two treatments.

90

91 **2. Materials and Methods**

92 **2.1. Recording and Noise Playback Protocol**

93 The experiment was conducted on European robins between February and June 2011 in
94 Northern Ireland. To create playback stimuli, we recorded the songs of 18 European robin
95 males in quiet areas using a solid state recorder (Marantz PMD660, .wav format, sample
96 frequency 44.1 kHz, resolution 16 bit) connected to a Sennheiser ME 66/K6 microphone.
97 From each of the 18 recordings, songs for playback were selected from sonograms
98 (sample frequency = 44.1 kHz, FFT = 512, overlap = 93.75%, time resolution = 5.8 ms)
99 generated with Avisoft SASlab Pro (R. Specht, Berlin). To simulate an average singing
100 male with a song rate of 7 songs/min (Montague et al., 2013), we randomly selected 21
101 songs of each recording to create playback files of 3 min duration. Songs for each
102 playback were arranged in Audacity (1.2.6) and normalised to the peak amplitude. A
103 copy of each playback file was merged with a standardised traffic noise recording
104 obtained from motorway bridges during rush hours (for details see (Gross et al., 2010)).
105

106 The experiment comprised two treatments: playbacks of the same stimulus songs
107 with and without traffic noise. As subjects we chose males in quiet areas, different from
108 those recorded to create the stimuli. Each of the 18 subjects received both treatments,
109 separated by a 3 minute silent interval. Each subject's singing behaviour was recorded
110 during the two three minute playback treatments with the same equipment as described
111 above. Treatment order was randomised, with the constraint that treatments were
112 balanced (Milinski, 1997). Background noise levels (dB(A)) were measured with a digital
113 sound-level metre SL-100 (Votcraft, Hirschau). Background noise levels in territories
114 where experiments were conducted were below 50 dB(A).

115

116 Stimuli were played from a Marantz PMD660 connected to a SME-AFS
117 loudspeaker (Saul Mineroff Electronics, USA) positioned 15-20 m from the subject's
118 song post, facing the subject, without obstacles in between. The volume of the stimuli
119 was adjusted before playback to 80 dB(A) at 1 m, as measured with the sound-level
120 meter. To analyse singing responses of the 18 subjects, we randomly selected 10 songs
121 from each recording in both treatments (McLaughlin and Kunc, 2013). For each song, we
122 measured (i) minimum frequency (kHz), i.e. the lowest frequency of any syllable in the
123 song; (ii) song complexity, i.e. the number of different elements; (iii) song length
124 (seconds); and (iv) song rate, i.e. the number of songs per minute. For a detailed
125 description of acoustic measurements see (Slabbekoorn and Peet, 2003; Hu and Cardoso,
126 2009; Verzijden et al., 2010; Francis et al., 2011; McLaughlin and Kunc, 2013; Montague
127 et al., 2013).

128

129 It is important to note that the aim of our study was to test how noise affects the
130 receiver's response during a vocal interaction, and not how singing behaviour differs
131 between an individual singing on its own during low and high levels of noise (c.f.,
132 Halfwerk and Slabbekoorn, 2009; Gross et al., 2010; Verzijden et al., 2010; Bermudez-
133 Cuamatzin et al., 2011; Hanna et al., 2011; McLaughlin and Kunc, 2013; Montague et al.,
134 2013).

135

136 **2. 2. Statistical Analysis**

137 To test whether the presence of ambient noise affected receivers' responses, we
138 used paired t-tests in R (2011) for each song parameter.

139

140

141 **3. Results**

142 Males' singing behaviour differed between the two playback treatments. During the
143 playback of song with noise, males sang at a higher minimum frequency ($t_{17} = -7.1$, $p <$
144 0.001 , Fig. 2a) than during the playback of song without noise. Males also sang less
145 complex songs ($t_{17} = 2.7$, $p = 0.01$, Fig. 2b), and shorter songs ($t_{17} = 3.3$, $p = 0.004$, Fig.
146 2c) during the playback of song with noise than during the playback of song without
147 noise. However, song rate did not differ significantly between the two treatments ($t_{17} =$
148 1.5 , $p = 0.2$, Fig. 2d).

149

150 **4. Discussion**

151 To our knowledge, this is the first experimental evidence in the wild that changes in
152 ambient noise levels affects vocal interactions. Thus, the whole process of
153 communication is affected by noise, not just the behaviour of the sender. Adjustments to
154 changes in the acoustic environment can affect the outcome of communication, because
155 even slight signal adjustments decrease transmission efficiency as well as individual or
156 species recognition (Wiley and Richards, 1982; Nelson, 1989; Mockford and Marshall,
157 2009; Mockford et al., 2011).

158

159 The adjustments of different song parameters may affect the outcome of male-
160 male competition and female choice. In some species, for example, low-frequency song is
161 correlated with fighting ability, and females prefer males singing at lower frequencies
162 (ten Cate et al., 2002; Cardoso, 2012). Moreover, complex and/or long songs are
163 advantageous in repelling opponents as well as in attracting females (Catchpole and

164 Slater, 2008). Therefore, males responding to a rival in a noisy environment face a
165 human-generated trade-off between producing a signal that is effective at repelling other
166 males and attracting females, versus a signal that is effective in noisy conditions.
167 However, we show that ambient noise causes the receiver to respond to an opponent with
168 less complex and shorter songs. Thus, changes in the acoustic environment affect both the
169 signal of the sender (Cunnington and Fahrig, 2010; Gross et al., 2010; Verzijden et al.,
170 2010; Bermudez-Cuamatzin et al., 2011; Hanna et al., 2011; Montague et al., 2013) but
171 also the receiver's response to the signaller. These changes in signal characteristics of
172 both sender and receiver could have far reaching consequences because animals exchange
173 information about their quality, status or motivation during vocal interactions (Todt and
174 Naguib, 2000; Vehrencamp, 2000). Changes in the dynamics of such interactions may
175 affect the ability of males to mediate conflicts between each other and the choice of
176 females (Mennill, Ratcliffe and Boag, 2002; Mennill et al., 2003; Kunc, Amrhein and
177 Naguib, 2006; Schmidt et al., 2006; Kunc et al., 2007). This is in line with a recent
178 finding in fish, where agonistic behaviour was influenced by anthropogenic noise
179 (Sebastianutto et al. 2011). Thus, environmental changes may affect not only sexually
180 selected traits, such as bird song per se, but also social interactions between individuals.

181

182 Adjustments to changing environmental conditions can occur through either
183 phenotypic plasticity or micro-evolutionary responses to natural selection (West-
184 Eberhard, 1989; Pigliucci, 2005; Charmantier et al., 2008). A growing body of
185 experimental studies show that adjustments of the sender in signalling to changes in the
186 acoustic environment are based on phenotypic behavioural plasticity (e.g. Gross et al.,

187 2010; Verzijden et al., 2010; Bermudez-Cuamatzin et al., 2011; Hanna et al., 2011;
188 Montague et al., 2013). In contrast to previous noise exposure experiments which were
189 confined to playback of anthropogenic noise we additionally played back the song of a
190 conspecific. Therefore, receivers also show a plastic response over a remarkably short
191 time scale to changes in the acoustic environment. Interestingly, the adjustments in song
192 characteristics found in this study are similar to the adjustments reported recently in
193 robins when singing alone (McLaughlin and Kunc, 2013; Montague et al., 2013). This
194 suggests that the adjustments in song characteristics during vocal interactions and in
195 situations in which an individual is singing alone have a similar underlying mechanism.

196

197 Regarding the behavioural adjustments observed in our experiment, a number of
198 possible mechanisms may be involved. Birds may increase the minimum frequency in
199 response to increasing noise levels (Slabbekoorn and Peet, 2003), and/or they may sing
200 louder (Brumm 2004; Nemeth and Brumm, 2010). A correlational study showed that in
201 blackbirds amplitude is positively correlated with minimum frequency and peak
202 frequency (Nemeth et al. 2013). A recent experimental study, however, demonstrates that
203 birds can adjust the frequency of their song independently of the songs amplitude (Potvin
204 and Mulder, 2013). A more complex analysis including more song characteristics,
205 although not song amplitude, has shown that the plastic response of minimum frequency
206 in response to increasing noise level restricts the elaboration of other song characteristics
207 such as song complexity (Montague et al. 2013). Taken all these results together, birds
208 adjust their songs in response to increasing noise levels irrespective of whether they sing
209 on their own or whether they are involved in a vocal interaction. This suggests that vocal

210 responses are more affected by changes in the acoustic environment rather than by the
211 sender's signal.

212

213 In conclusion, our study provides evidence that individuals adjust their signals
214 during vocal interactions to changes in the acoustic environment. Anthropogenically
215 induced changes in acoustic signals may have fundamental consequences, because
216 animals exchange information on their quality, status or motivation during vocal
217 interactions. Therefore, changes in the entire communication process have to be
218 considered to understand how species are affected by anthropogenic changes in the
219 acoustic environment.

220

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225

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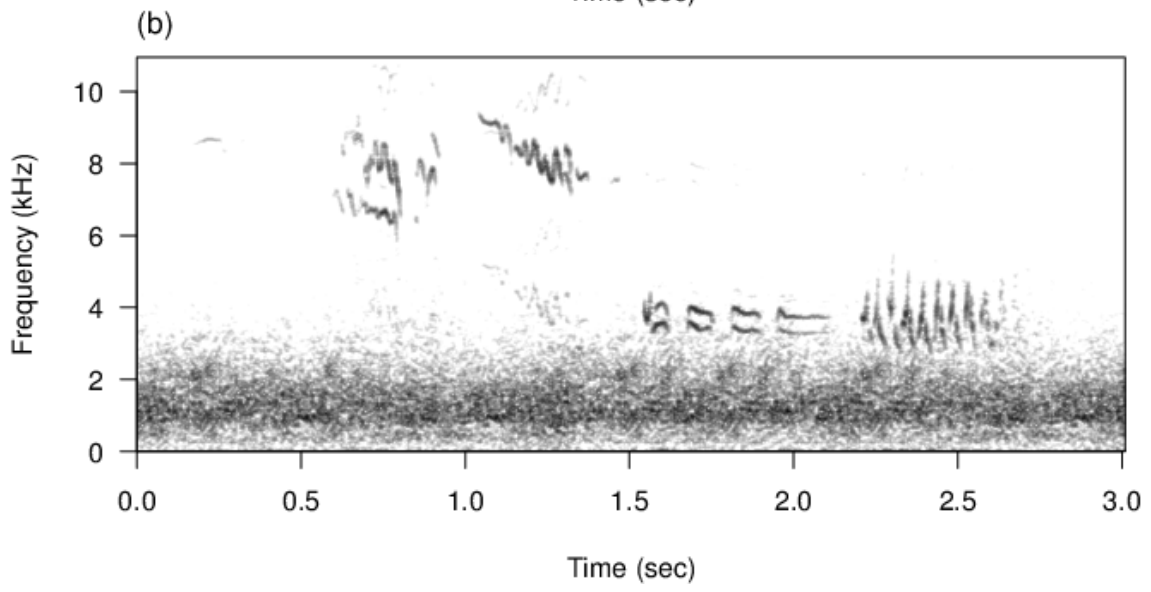
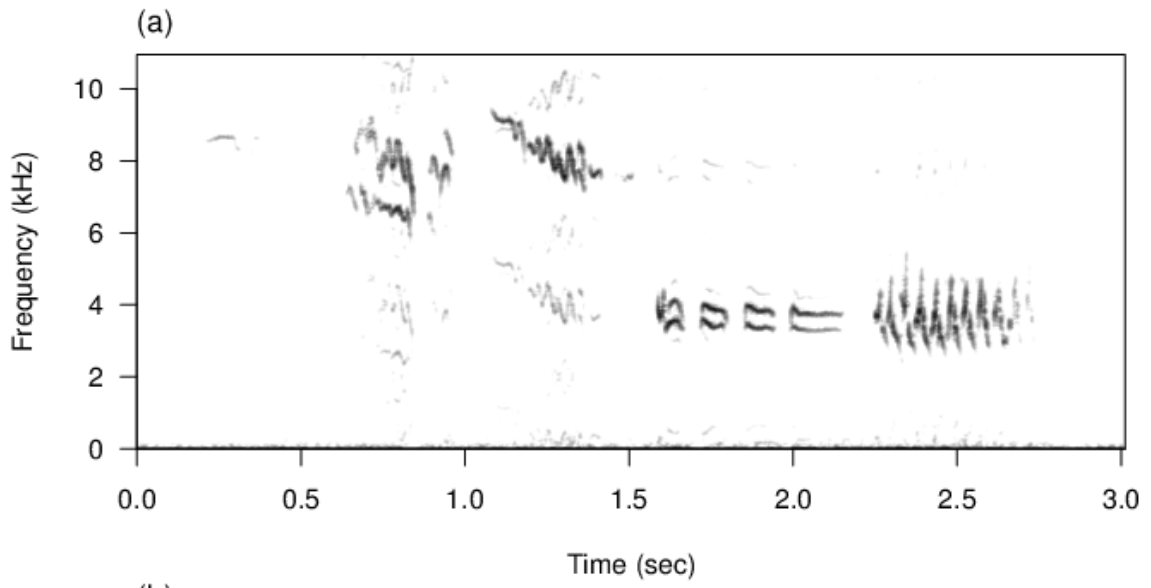
321 **Fig. 1** Sonagrams of song stimuli used of a European robin played back as (a) song
322 without anthropogenic noise and (b) song with anthropogenic noise.

323

324 **Fig. 2** Mean \pm SE (a) minimum frequency, (b) song complexity, (c) song duration, and
325 (d) song rate of individuals responding to playback of conspecific song without (white
326 bars) and with anthropogenic noise (grey bars).

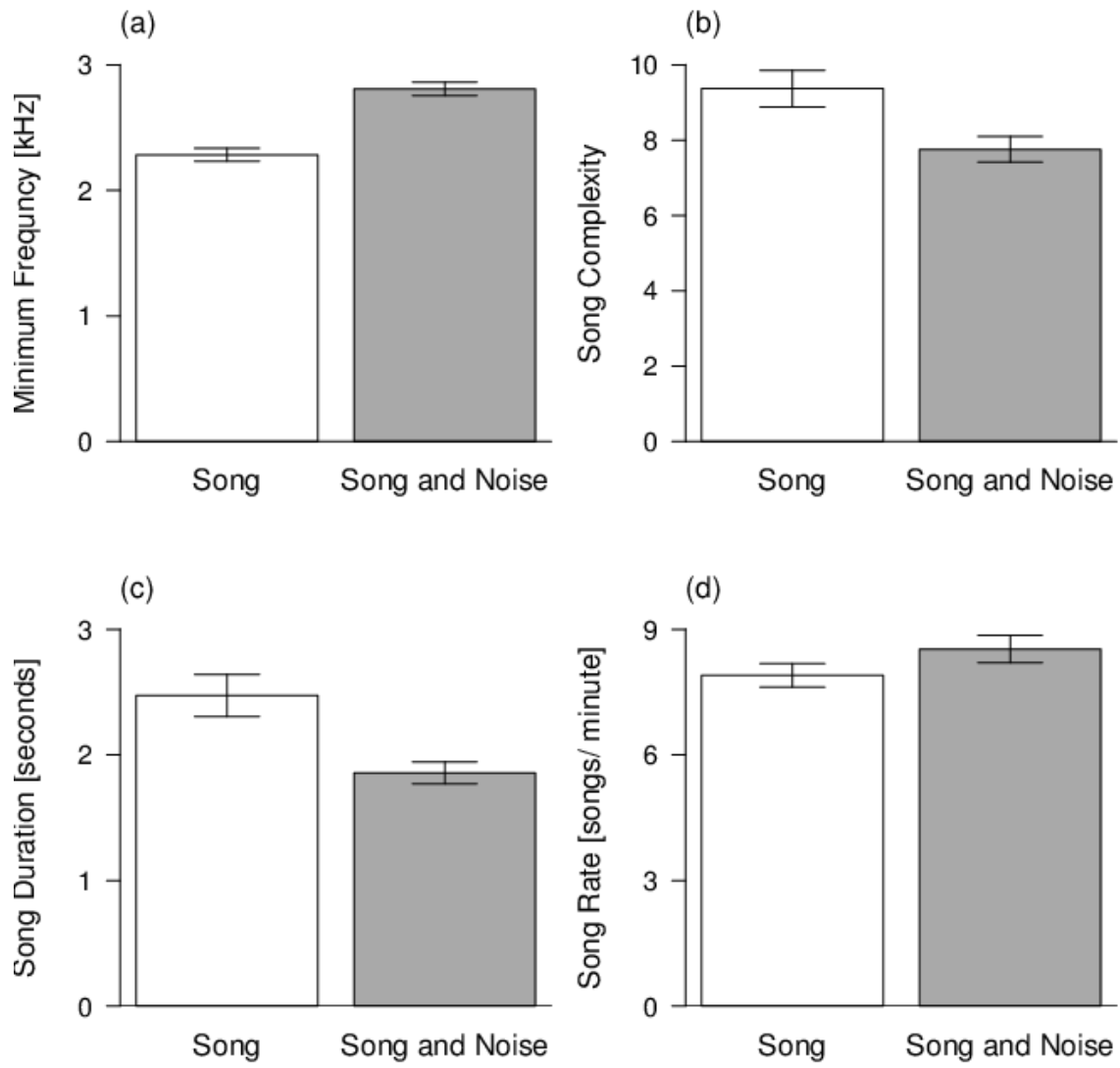
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