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2

3 **Title: Aircraft sound exposure leads to song frequency decline and elevated aggression**
4 **in wild chiffchaffs**

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17 Keywords: Aircraft noise, bird song, aggression, masking, *Phylloscopus collybita*

18

19 **Abstract:** 1. The ubiquitous anthropogenic low-frequency noise impedes communication by
20 masking animal signals. To overcome this communication barrier, animals may increase the
21 frequency, amplitude and delivery rate of their acoustic signals, making them more easily
22 heard. However, a direct impact of intermittent, high-level aircraft noise on birds' behaviour
23 living close to a runway has not been studied in detail.

24 2. We recorded common chiffchaffs *Phylloscopus collybita* songs near two airports and
25 nearby control areas, and we measured sound levels in their territories at Manchester airport.
26 The song recordings were made in between aircraft movements, when ambient sound levels
27 were similar between airport and control populations. We also conducted playback
28 experiments at the airport and a control population to test the salience of airport, and control
29 population specific songs.

30 3. In contrast to the general pattern of increased song frequency in noisy areas, we show that
31 common chiffchaffs at airports show a negative relationship between noise exposure level
32 and song frequency.

33 4. Experimental data show that chiffchaffs living near airports also respond more
34 aggressively to song playback.

35 5. Since the decrease in song frequency results in increased overlap with aircraft noise, these
36 findings cannot be explained as an adaptation to improve communication. The increased
37 levels of aggression suggests that chiffchaffs, like humans, might be affected behaviourally
38 by extreme noise pollution. These findings should influence environmental impact
39 assessments for airport expansions globally.

40

41

42

43 **Introduction**

44 Animals, like humans, are negatively affected by the global increase in anthropogenic noise
45 levels (Barber, Crooks & Fristrup 2010; Shannon *et al.* 2016). For wildlife, anthropogenic
46 noise leads to displacement, disrupts parent-offspring communication, increases stress-related
47 hormone levels and vigilance behaviour and changes communication systems (Rich &
48 Romero 2005; Barber, Crooks & Fristrup 2010; Kight & Swaddle 2011). Noise exposure in
49 humans has been linked to hearing loss, tinnitus, hypertension, sleep deprivation, and
50 increased stress levels (Huss *et al.* 2010; Basner *et al.* 2014; Stansfeld & Shipley 2015).
51 Anthropogenic noise at the current level and scale is a pervasive (Buxton *et al.* 2017) and
52 relatively novel selection pressure that is projected to increase with human population
53 expansion (Barber, Crooks & Fristrup 2010). The capacity of animal species to adapt to this
54 novel selection pressure affects their distribution, which contributes to their success as urban
55 adapters (Slabbekoorn 2013).

56

57 Anthropogenic noise sources differ in their acoustic structure and temporal presence and they
58 may have different effects on wildlife (Gill *et al.* 2015). Motorways produce diel patterns of
59 peaks and troughs in sound level and reach maximum levels of approximately 65dB(A) along
60 the linear structure of the road with the spectral energy concentrated below 2kHz (Halfwerk
61 *et al.* 2011b). Industries, such as resource extraction and construction usually provide a point
62 source of noise and thus affect restricted areas. However, their sound levels can reach up to
63 75-90dB(A) (Habib, Bayne & Boutin 2007). Trains and aircrafts produce intermittent noise,
64 interspersed with periods of relative quiet. Aircrafts movements can reach extreme noise
65 levels of over 100dB(A), at 100m distance from an aircraft taking off (Goudie & Jones
66 2004).

67 Noise interferes with acoustic communication between animals through the masking of their
68 signals. Masking decreases the Signal to Noise Ratio (SNR) of an acoustic signal, reducing
69 the available transmission distance and thus making communication less effective (Lohr,
70 Wright & Dooling 2003). Animals have essentially three strategies to counteract the masking
71 effect of anthropogenic noise. They can increase the amplitude of their signals and thus
72 increase the SNR, a process known as the Lombard effect and observed in many animals
73 (Brumm 2004). The capacity to increase the SNR depends on the level of masking noise and
74 the flexibility of animal species to increase their signal amplitude. A second strategy involves
75 changing the delivery time of the signals to avoid the temporal overlap between signal and
76 noise (Fuller, Warren & Gaston 2007; Arroyo-Solís *et al.* 2013). A third strategy relies on the
77 species' capacity to change the acoustic structure of their signals to facilitate masking release.
78 When exposed to low-frequency anthropogenic noise, animals may increase the frequency of
79 their acoustic signals, rather than the amplitude as in the Lombard effect (Slabbekoorn & Peet
80 2003), presumably to reduce the effect of masking. Noise-dependent upward frequency shifts
81 have been observed for a wide range of bird species (Slabbekoorn 2013).

82

83 To date only one study has addressed the impact of aircraft noise on bird song structure. In
84 contrast to other anthropogenic noise sources, the frequency of blackbird (*Turdus merula*)
85 songs did not differ between quiet and airport populations (Sierro *et al.* 2017a). An
86 explanation for this is that frequency adjustment is not an effective strategy as aircraft sound
87 levels may exceed the capacity for most if not all animals to increase the signal-to-noise ratio
88 sufficiently to be heard. Birds move away from continuous noise at airfields (Swaddle *et al.*
89 2016) and reduce singing when their songs are masked by aircraft noise above 78dB(A) SPL
90 (Dominoni *et al.* 2016). However, aircraft noise is intermittent and thus birds can use quiet
91 phases in between aircraft movements to communicate. This strategy would require no

92 spectral adjustment to the song to maintain signal efficacy. Indeed, when exposed to aircraft
93 noise birds adjust the onset of dawn singing to avoid peak aircraft-movement times and
94 reduce overlap with aircraft noise (Gil *et al.* 2014; Dominoni *et al.* 2016; Sierro *et al.* 2017b).
95 Nevertheless, many birds remain in their territories throughout the daily cycle of aircraft
96 movements, and continue singing even in peak aircraft-movement times.

97

98 Here we compared song structure of common chiffchaffs (*Phylloscopus collybita*) at two
99 different airports (Manchester and Amsterdam) and two control sites. We also measured
100 aircraft sound levels in chiffchaff territories at Manchester airport and related these to song
101 characteristics of individual chiffchaffs. The song recordings at the airports were made in
102 between aircraft movements. Having demonstrated that the songs of chiffchaffs exposed to
103 aircraft noise decreased in spectral parameters, we then proceeded to investigate whether the
104 spectral change was biologically relevant. Spectral and temporal properties of bird song
105 convey information about body condition, status and motivation to fight (Gil & Gahr 2002)
106 and play an important role in mate attraction and territory defence (Catchpole & Slater 2003).
107 When these parameters change, this may also affect the signal value of the songs (de Kort *et*
108 *al.* 2009a; Halfwerk *et al.* 2011a) in the context of sexual selection. This raised the question
109 whether the airport songs that differ in acoustic properties from the control songs are
110 effective in territory defence. To that end, we conducted playback experiments at Manchester
111 airport and a nearby control location.

112

113

114 **Materials and Methods**

115

116 **Study site and species** The main study sites were Manchester Airport, UK (53.351039, -
117 2.279860) and Woolston Eyes nature reserve (53.389471, -2.528626) as a control site, 20 km
118 to the south east. Additional sound recordings were obtained from Schiphol airport,
119 Netherlands (52.317438, 4.823373), and Meijendel nature reserve (52.126934, 4.340512) as a
120 control site, approximately 50 km to the south-west from the airport. Manchester airport has
121 approximately 490 aircraft movements on two runways a day (CAA 2015), while Schiphol
122 airport has approximately 1200 aircraft movements on six runways a day (Airport Council
123 International 2015). At Manchester airport this study focused on the area around runway 2
124 that contributed 85% of all aircraft movements in 2014 (MAG Departure information pack
125 2017). All study sites are characterised by scrublands surrounding small patches of broadleaf
126 woodland, with willow (*Salix sp.*), hazel (*Corylus*), sycamore (*Acer pseudoplatinus*) and oak
127 (*Quercus sp.*) being the dominant tree species.

128 Chiffchaffs are summer migrants to Europe, with the first males usually arriving in March.
129 Males defend their territories by singing from strategic positions throughout the breeding
130 season, which typically concludes at the end of June. Male chiffchaffs mediate social
131 interactions by modifying temporal and spectral song parameters. Fighting ability is signalled
132 with a relatively low peak frequency (Linhart, Slabbekoorn & Fuchs 2012), whilst duration of
133 songs signals motivation to fight (Linhart *et al.* 2013). Chiffchaffs can shift song frequencies
134 immediately in response to anthropogenic noise (Verzijden *et al.* 2010). The start of the dawn
135 chorus in chiffchaffs does not differ between quiet sites and those exposed to aircraft noise
136 (unpublished data).

137 **Noise measures** Noise level measurements for UK sites were obtained between 06:30

138 and 12:00 from March to June 2014. To obtain sound levels, the maximum level with A-
139 weighted frequency response and fast time constant (LAFmax) for each of the chiffchaff
140 territories in the UK was measured using a sound level meter (Precision Gold N05CC), set at
141 1.5m from the ground. In addition, average ambient noise levels (L_{Aeq} (t)) were obtained by
142 recording sound levels every second for a 10-minute period using a class 2 industry standard
143 sound level meter (Casella CEL-246, Fast response, A weighted). Where possible the noise
144 level meters were tripod mounted at a height of 1.5 meters, facing vertically upwards directly
145 underneath the singing post. Where a tripod could not be positioned directly underneath the
146 singing post, the closest open space was selected. Noise levels were compared between sites
147 with a two-tailed, independent t-test. Additionally, L_{Aeq}(t) were compared between airport
148 and control sites in between aircraft movements. The 10-minute sound level recordings
149 consist of 600 measurements, and each measurement that exceeded background noise levels
150 and could be attributed to aircraft movement (generally above 60dB(A)), was removed to
151 generate L_{Aeq} for airport sites without aircraft noise. Sound level data for the sites in the
152 Netherlands were not collected for this aspect of the study.

153

154 **Song recording and analysis** Song recordings were made between 06:30 and 12:00 from
155 March 17 to June 30, 2014 near Manchester Airport and Woolston Eyes nature reserve on
156 alternate days. The distance between the territories of recorded individuals and the runway
157 ranged between 180m to 2100m at the Manchester airport site. The recordings for Schiphol
158 airport and Meijendel nature reserve were made in May 2015. Each 10-minute recording
159 session was preceded by a 5-minute habituation period to reduce the effect of observer
160 presence on singing behaviour. To reduce the chance of recording the same individual twice,
161 no song recordings were made within 200m of another recorded individual. This distance
162 between territories is twice the recorded territory size in chiffchaffs (Rodrigues 1998). In

163 some cases, whilst recording one individual, another bird was observed singing and in that
164 case the second bird may have been recorded closer than 200 m. Each individual chiffchaff
165 was recorded from a maximum distance of 10 m and the bird was always in sight of the
166 recorder. Recordings were made using a Sennheiser ME67 microphone and a Marantz
167 PMD661 MKII digital recorder (sampling frequency: 44100 Hz; 16 bit; WAV format). For
168 each recorded individual a random sample of ten songs was selected from the 10-minute
169 recording using the sample function, without replacement, in R (R core team, 2016). Because
170 of the inherent difficulties in obtaining accurate frequency measurements during noise events
171 (Verzijden *et al.* 2010; Brumm *et al.* 2017), only songs recorded in between aircraft
172 movements were used for song analysis. This is important to note because this means that
173 during the song recording, ambient sound levels were not affected by aircraft movements.
174 Four spectral and three temporal parameters for each song were measured using the
175 automatic parameter measurement feature in Avisoft-SAS Lab Pro version 4.3 (Avisoft
176 bioacoustics, Berlin, Germany). The automatic parameter measurement feature allows for
177 objective measurements across the different recordings and is independent of recording
178 quality. For element separation an automatic single threshold of -21 dB was used with a hold
179 time of 100 ms (spectrogram settings: Hamming window FFT-size = 512, overlap 50 %). The
180 spectral parameters measured were maximum, minimum, and peak frequency, and frequency
181 bandwidth, and the temporal parameters were syllable and song duration, and number of
182 syllables.

183

184 Two types of analyses were conducted on the song parameters. The first tests for song
185 structural differences between airport and control birds. Song parameters were compared as a
186 function of site (airport or control site) using linear mixed effects models with country (UK
187 or Netherlands) as a random factor. Mixed effects models were compared to null models with

188 no random effects using an ANOVA. Models were validated by inspection of residual plots.
189 Post-hoc Tukey tests were used to further explain any significant results. All p values
190 reported are adjusted values following sequential Bonferroni correction for multiple testing
191 (Rice 1989).

192 The second type of analysis tests for a relationship between LAFmax as measured in an
193 individual's territory and the 6 song parameters. This analysis was done separately for the
194 Manchester airport population and the control population, and did not include the data from
195 the Netherlands. For the comparison within sites MANOVA models with LAFmax and Julian
196 date as independent factors were used. Julian date was included to control for seasonal
197 variation in song parameters (Vehrencamp *et al.* 2013). Model selection was based on the
198 lowest Akaike Information Criterion (AIC) value (Zuur *et al.* 2009).

199

200 **Syllable type** Initial visual inspection of spectrograms of chiffchaff songs for both UK
201 populations suggested 7 different syllable types (Figure 1). Discriminant function analysis
202 (DFA) was used for objective categorization of syllable types. Twenty random samples of
203 each syllable type were selected using the R sample function with no replacement. A
204 discriminant function separated the syllable types based on maximum, minimum, and peak
205 frequency and syllable length for a subset ($n=10$) of each syllable type. The function was then
206 used to categorise the remaining 10 syllables for each type. The proportion of observed
207 syllable types was compared to the proportion of predicted syllable types to test the accuracy
208 of the DFA. Two syllable types (c and d, see Figure1) were not discriminated by the function
209 and these were merged, leaving 6 distinct syllable types. The categorisation was then used to
210 assess the average proportion of each syllable type within the songs of chiffchaffs at the
211 airport and control sites. The difference between the two sites was tested with a Wilcoxon
212 signed-ranks test.

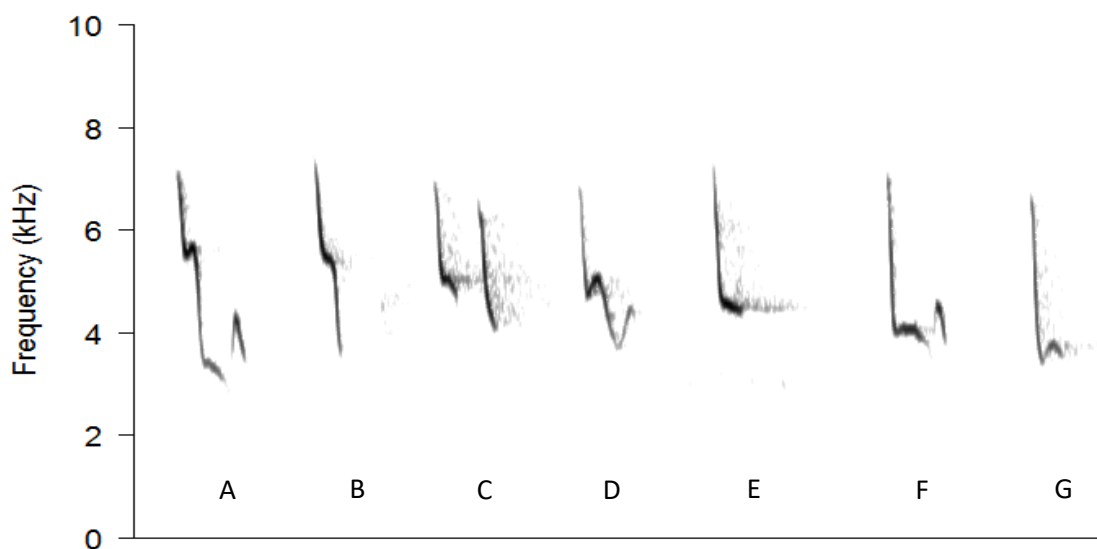


Figure 1: Spectrogram of all syllable types of chiffchaff songs (*Phylloscopus collybita*) recorded in the UK. Syllables are order ranked from highest to lowest peak frequency. Following discriminant function analysis, syllable types C and D were merged. Figure spectrogram settings: Hamming window, FFT size 256 and overlap of 87.5%.

213

214 **Playback procedure** Playback trials were conducted between 6:00 and 11:00 from March
 215 31- April 19, 2015 in the UK sites. A remotely controlled loudspeaker (Fox Pro Fury,
 216 www.gofoxpro.com) was placed in a tree at approximately 1.8 m height within the territory
 217 of a subject. All observations were conducted from a camouflaged pop-up hide positioned
 218 approximately 10 m from the loudspeaker, which the observer entered at least five minutes
 219 before start of playback.

220 **Playback design** The stimuli were created from songs recorded from 22 males (N=11
 221 Manchester airport, N=11 control site). Songs were randomly selected using the sample
 222 function with replacement in R (R core team 2016) from a database of recordings made in
 223 2014. The songs of the birds at the airport contain fewer high notes (i.e. note 'A', see Figure
 224 1 and results) and more low notes (note 'G') than the songs of control birds. Thus, to create
 225 pairs of stimuli that were identical, except for the proportion of high and low notes we
 226 replaced the high A-type syllable with the low G-type syllable from the same song to create

227 an airport type song. Similarly, to create a control type stimulus, we replaced the low G-type
228 syllable with the high A-type syllable from the same song. Only songs that contained both
229 airport type (G type) and control type syllables (A type) were used for stimulus preparation,
230 and both control and airport population contributed the same number (11) of original
231 recordings.

232

233 Song files were band-pass filtered (1000-9000 Hz) and the amplitude was normalized to 90%
234 of the maximum amplitude in Avisoft-SASlab (Specht. R, Berlin, Germany). The procedure
235 ensured that song lengths and syllable rates of the manipulated songs did not differ from
236 those for the original recordings or between airport type or control type stimuli within a pair
237 of stimuli. Each subject was exposed to a pair of stimuli derived from the same original song
238 and the stimuli only differed in the proportion of high/low notes. This procedure precludes
239 other song variables, such as duration or delivery rate, to affect the response of the birds.

240 Each playback trial was divided into three 120-second observation periods. The pre-playback
241 period (120s of silence) was the baseline period for that subject, followed by two exposure
242 periods (120s) consisting of 30s of playback followed by 90s of observation each. The order
243 of playback stimulus type (airport and control) alternated between subjects. Behavioural
244 responses were recorded using a data logging application (SpectatorGo!

245 http://www.biobserve.com/products/spectator_go/) on a touch screen device (iPod touch:
246 www.apple.com). Subject responses were assessed with three behavioural variables: (1)

247 attack = the number of times the individual came into physical contact with the loudspeaker,
248 (2) flight = the number of times the subject flew within 2m of the loudspeaker, (3) song = the
249 number of times the subject vocalised. Each playback trial was conducted on a different
250 subject. Birds in adjacent territories were not tested in the same 24hr period to avoid

251 carryover effects. All subjects at the airport (N=33) and control site (N=33) were tested for
252 both stimuli.

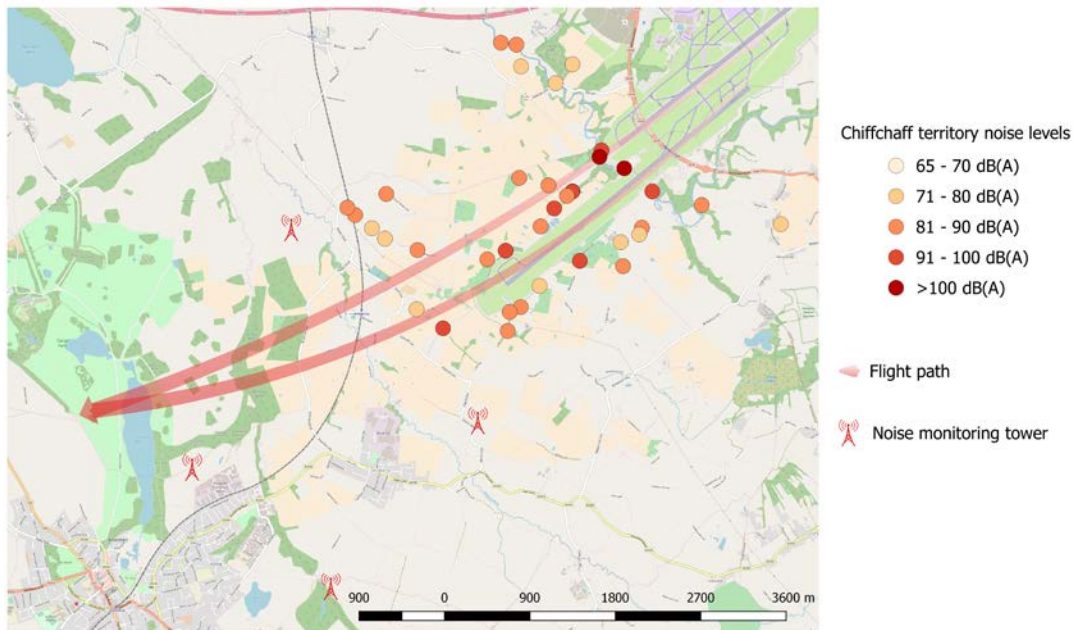
253 **Statistical analyses** Generalised linear models assuming Poisson distributions and using a
254 log link function were built to assess the effect of stimulus type on the response measures. To
255 control for effect of seasonality or location of original recording, Julian date and recording
256 site (airport or control) were included as additional independent variables. Model selection
257 was based on Akaike's Information criteria (AIC) for each model (Zuur et al. 2009).
258 Sequential Bonferroni corrections were applied to control for the increased probability of
259 type 1 errors as a result of multiple testing (Rice 1989). Cross-over (Díaz-Uriarte 2002) and
260 order effects were tested for with Mann-Whitey U tests and Wilcoxon signed rank tests,
261 respectively.

262

263 **Results**

264 **Sound exposure levels**

265 Sound levels generated by aircraft movements measured at chiffchaff territories at
266 Manchester airport varied between LAFmax 67 and 118 dB(A) (mean LAFmax =
267 81.93dB(A) \pm SDE = 9.11, see Figure 2), while at the control site sound levels varied
268 between LAFmax = 42 and 67.3 dB(A) (mean LAFmax = 57.13 dB(A) \pm SDE 4.57). The
269 mean LAFmax sound levels differed between the airport and control territories ($T= 12.70$,
270 $p<0.001$). The LAeq sound levels at the airport territories measured over a 10 minute period
271 that included aircraft noise varied between 51 and 67 dB(A) (mean LAeq = 58.5 dB(A) \pm
272 SDE = 4.51). The LAeq recorded at Manchester airport territories in between aircraft
273 movements ranged from 43.0 to 56.5 dB(A) (mean LAeq = 47.91 dB(A) \pm 3.45 SDE) and did
274 not differ to ambient noise levels at the control site (Control Min LAeq = 42.90, Control Max
275 LAeq = 51.0, Control mean LAeq = 46.42 \pm 2.59 SDE ; t-test: $T = 1.72$, $p = 0.09$).



277

278

279 **Figure 2:** Map of the study area around Manchester airport indicating the location and sound
 280 level of the chiffchaff territories sampled for this study. The main aircraft flight path from each
 281 runway, and the location of noise monitoring towers are indicated.

281

282 **Song structure at airports and control site** When comparing the average song parameters

283 between airport and control populations, we included individuals from Manchester airport

284 (N=38) and control site (N=30) and additional recordings from Schiphol airport (N=18) and

285 control site (N=15). Chiffchaffs at airport sites show a lower average song Maximum

286 frequency ($F_{3,100} = 9.86, p < 0.001$). This was replicated at the population level, at

287 the two widely separated airports (UK airport vs UK control: $Z = 2.461, p = 0.042$; NL

288 airport vs NL control: $Z = 2.741, p = 0.024$) (Figure 4). There was also significant variation in

289 peak frequency ($F_{3,100} = 8.77, p < 0.001$) between sites; airport birds in the UK used lower

290 peak frequencies than control birds (UK control vs UK airport: $Z = 2.461, p < 0.001$). In the

291 Netherlands no difference in peak frequency between the control and the airport population

292 was detected (NL control vs NL airport: $Z = 2.741, p = 0.355$), although the numerical

293 difference was in the same direction (Figure 3). Overall, there was significant variation in

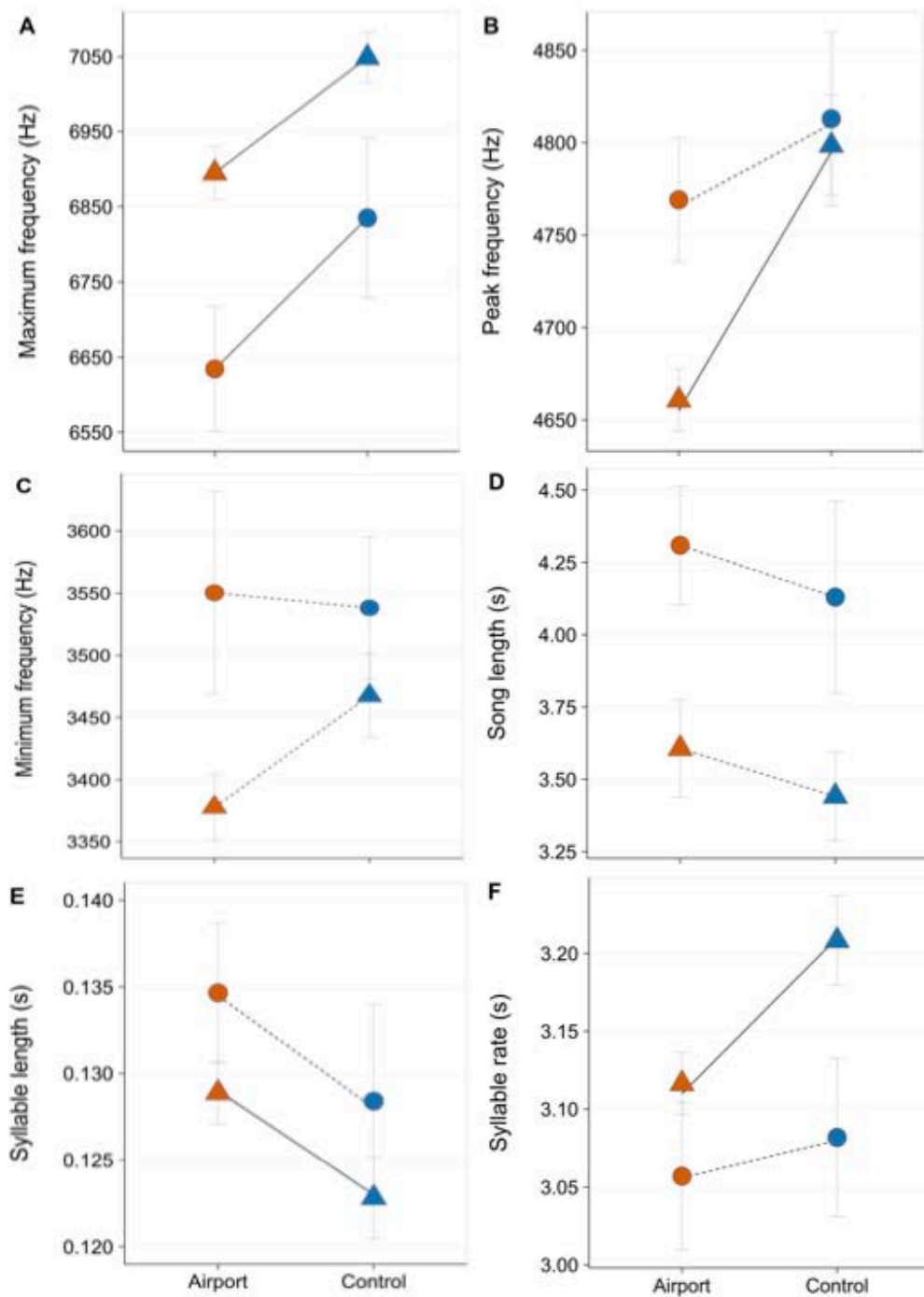
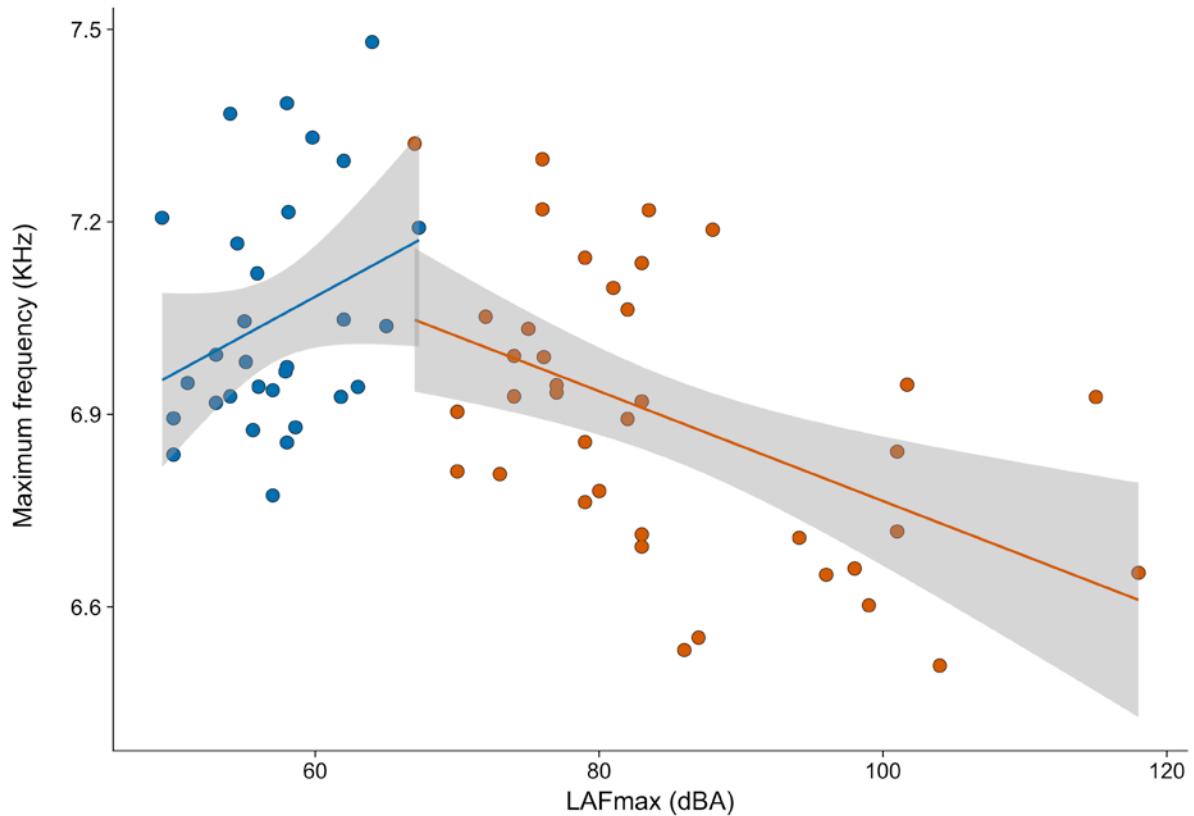


Figure 3: Comparison of Mean (\pm SEM) of six chiffchaff (*Phylloscopus collybita*) song parameters recorded at two airports (orange, Manchester N= 38, Schiphol, N=18) and quiet control sites (blue, Woolston eyes nature reserve N=30, and Meijendel nature reserve N=18). Unbroken lines indicate significant differences between airport and control sites within a country, while dotted lines indicate non-significant differences.

295 minimum frequency between sites ($F_{3,100} = 8.77, p = 0.03$). Posthoc analyses showed that this
296 difference could be attributed to NL airport and UK control sites ($Z = -2.802, p = 0.031$).
297 Overall Chiffchaffs in the Netherlands used lower maximum frequencies but higher peak
298 frequencies than those in the UK (Figure 3), a level of geographic variation that is not
299 unusual between distant populations of the same species (Slabbekoorn & Den Boer-Visser
300 2006; Podos & Warren 2007). Syllable rate differed between sites ($F_{3,100} = 24.18, p = 0.001$),
301 whilst this variation can be accounted for by differences between sites in different countries,
302 significant differences in syllable length were detected between UK control and UK airport
303 sites ($Z = 2.351, p = 0.038$). There was no significant variation in song length between any of
304 the sites ($F_{3,100} = 4.024, p = 0.09$). The variables ‘Number of syllables’ and ‘Frequency
305 bandwidth’ were removed from further analysis because they were highly correlated with
306 ‘Song length’ and ‘Syllable duration’ ($r > 0.80$) and with ‘Peak frequency’ and ‘Maximum
307 frequency’ ($r > 0.60$), respectively.

308

309 **Song structure and aircraft noise levels** A detailed spectral analysis of songs at the
310 individual level around Manchester airport ($N=38$) showed a significant decrease in the
311 maximum frequency of chiffchaff songs with an increase in LAFmax ($N=38, F_{1,37} =$
312 $12.907, p = 0.001$). There was no effect on LAFmax on any other song
313 parameters in the airport population (Table 1). Congruent with other studies, there
314 was a positive correlation with minimum frequency and LAFmax detected at the quiet control
315 site ($N=30, F_{1,29} = 12.907, p = 0.001$, Figure 4). Control birds also sang at a slower rate
316 as LAFmax increased ($N = 30, F_{1,29} = 8.808, p = 0.006$). There was no effect of
317 LAFmax on any other song parameter in the control population. Julian date had
318 no effect on any of the temporal or spectral variables at either airport or control sites (Table
319 1). The reduced maximum frequency in the songs of the airport population results from a



320

Figure 4: Maximum frequencies of the songs of individual common chiffchaffs (*Phylloscopus collybita*) around Manchester Airport (orange) and control site (blue). Maximum frequencies varied over a range of about 1000 Hz and were correlated with the maximum sound level (LAFmax) measured at the territory. Blue dots represent birds from the control site and show a positive correlation between the maximum song frequency and the maximum noise level (LAFmax) at their territory. Red dots represent airport birds and show a negative correlation between the maximum song frequency and the maximum noise level at their territory.

321

322 lower percentage of high-frequency syllable type A (airport= 12.7%, control= 20.4%,

323 $W=418.5$, $p=0.046$) and higher percentage of low-frequency syllable type G (airport = 18%,

324 control = 8%, $W= 761$, $p=0.014$) in the songs, rather than a complete downward spectral shift

325 of the songs. In other respects the syllable repertoires and relative syllable use was identical

326 between the two populations.

327

Table 1. Test statistics for MANOVA models used to explore the effects of LAFmax and season (Julian Date) on common chiffchaff (*Phylloscopus collybita*) song parameters at Manchester Airport (N=38) and Woolston Eyes nature reserve (control, N=30).

Parameters	Effect	Airport		Control	
		F	<i>p</i>	F	<i>p</i>
MaxF	LAFmax	12.907	0.0001	2.647	0.115
	Julian Date	6.078	0.018	0.021	0.885
MinF	LAFmax	0.152	0.699	4.554	0.042
	Julian Date	0.500	0.482	0.159	0.693
PeakF	LAFmax	0.373	0.545	0.850	0.364
	Julian Date	0.338	0.565	0.131	0.720
Syll. Length	LAFmax	0.109	0.743	8.808	0.006
	Julian Date	3.535	0.068	0.395	0.535
Syll. Rate	LAFmax	0.498	0.498	8.542	0.007
	Julian Date	3.365	0.075	2.487	0.126
Song length	LAFmax	0.001	0.980	0.004	0.945
	Julian Date	0.020	0.890	1.232	0.277

Notes: Bold values indicate significance following *p*-value adjustment for multiple testing. MaxF = Maximum Frequency (kHz), MinF = Minimum Frequency (kHz), PeakF = Peak Frequency (kHz), Syll. Length = duration of syllable (s), Syll. Rate = Number of syllables/ (s), Song length = Duration of song (s).

328

329 **Playback results**

330 Both airport and control stimuli elicited a strong response based on two behavioural response
331 measures in both the airport and control population. The airport population responded with a
332 reduced number of songs (control stimulus: $n=33$, $Z = -4.64$, $p < 0.001$; airport stimulus:
333 $n=33$, $Z = -4.83$, $p < 0.001$), and an increase in approach to the playback loud speaker
334 (control, $n=33$, $Z = 4.97$, $p < 0.001$; airport: $n=33$, $Z = 3.25$, $p = 0.001$), compared to baseline
335 behaviour during the pre-playback period. The control population responded similarly with a
336 smaller number of songs (control: $n=33$, $Z = -3.097$, $p = 0.002$; airport: $n=33$, $Z = -1.072$, $p =$
337 0.006) and an increase in approach to the playback loudspeaker (control: $n=33$, $Z = 3.57$, p
338 < 0.001 , airport: $n=33$, $Z = 2.09$, $p = 0.001$). However, although both populations clearly
339 responded to the stimuli, they did not show a difference in response to the two playback
340 stimuli for these 2 response parameters (all $p > 0.05$). Nevertheless, at the airport a fivefold
341 higher number of individuals (25/33) physically attacked the loudspeaker following playback

342 compared to control birds (5/33, Fishers exacts test: Airport N = 33, control, N =33, p
343 <0.001, Figure 5),. The airport population attacked the playback speaker more in response to
344 airport than control stimuli ($Z = 2.49, p = 0.03$), a pattern not displayed by the control
345 population. The difference in response is not an immediate result of exposure to aircraft
346 noise, as all trials were conducted when there were no aircraft movements.
347

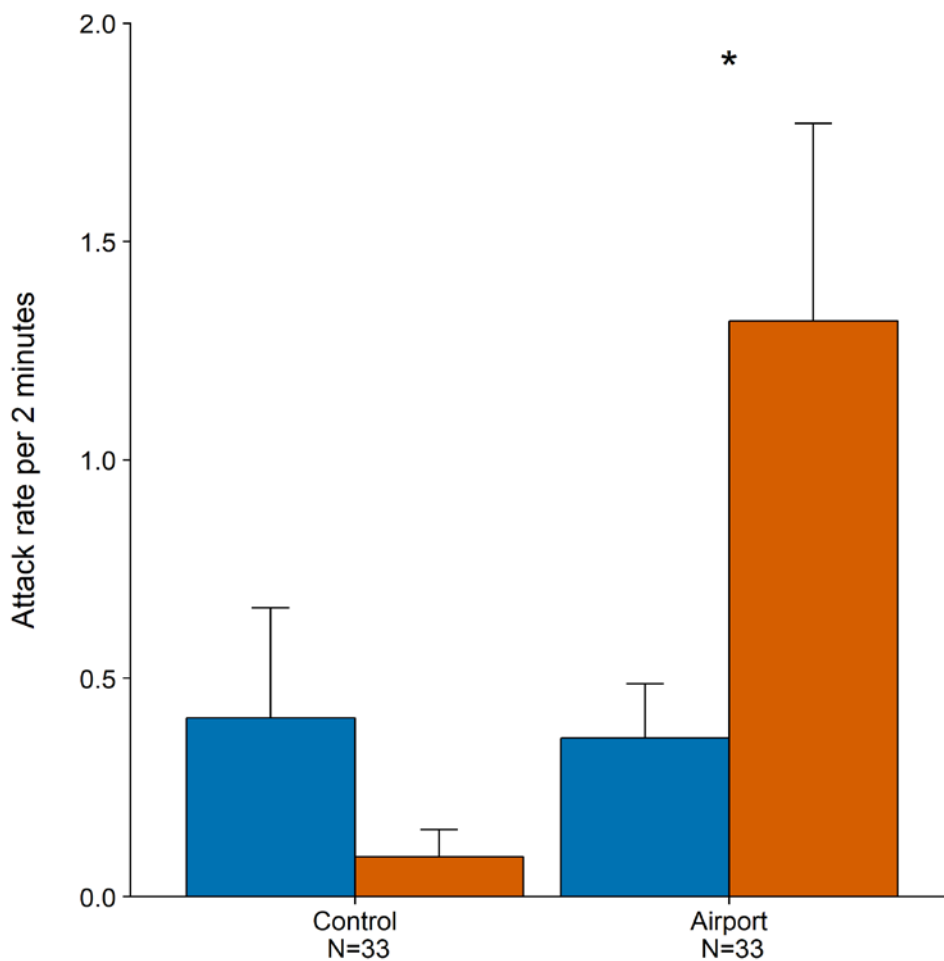


Figure 5 Average number of attacks per 120 s by common chiffchaffs on the playback loudspeaker broadcasting either control (blue) or airport (orange) type stimuli for the control population (left) and the airport population (right).

348
349
350

351 **Discussion**

352 Chiffchaffs holding territories near Manchester airport runway 2 are exposed to extreme
353 sound levels, frequently exceeding LAFmax of 110dB(A). These chiffchaffs sing songs
354 containing more low-frequency syllables with lower maximum and peak frequency and a
355 slower song rate than nearby control populations, and the spectral changes are replicated for
356 chiffchaffs living near Schiphol airport in the Netherlands. In addition, the maximum song
357 frequency decreases with increasing noise levels as measured in the birds' territories, while
358 the control population shows a positive relationship with more moderate territorial noise
359 levels, congruent with other studies (Slabbekoorn 2013). Both airport and control populations
360 respond strongly and indiscriminately to both airport type (low frequency) and control type
361 (high frequency) songs in two response parameters, showing that both stimulus types are
362 equally salient to the birds. However, a third response measure shows that the airport
363 population is more aggressive, with 5 times more individuals physically attacking the
364 playback loud speaker than the control population.

365

366 The sound levels measured at Manchester airport in this study are similar to those in a study
367 on the impact of aircraft noise on behaviour of harlequin ducks (*Histrionicus histrionicus*)
368 (Goudie & Jones 2004). Our measurements appear higher than those reported by the
369 Manchester Airport Noise Information System (MANTIS, see Table 1). However, the
370 MANTIS system reports Lden rather than LAFmax. In addition, although, Manchester airport
371 has 13 noise level meters around the airport, the closest of these (Mobbeley primary school
372 53.319662, -2.31352) is approximately 1.4km away from the nearest runway edge, whilst our
373 closest measurement is 186m from the runway. The U.S. department of Transportation,
374 Federal Aviation Administration provides modelled noise level data per aircraft type
375 (Burlison 2002). The loudest aircraft, the Boeing B-747-100 is estimated to produce 100.5

376 dB(A), while the quietest, a Cessna 152 is estimated to produce 55 dB(A) at a distance of
377 6.5km from the start of the take-off roll. Given that halving the distance from the aircraft
378 equals a 6dB increase in sound level, these values correspond to 130 dB(A) and 85.2 dB(A)
379 at 200m, respectively, which is in line with our measurements.

380

381 The lower song frequency and delivery rate of chiffchaffs at airports contrasts to that reported
382 in most other studies on the impact of anthropogenic noise on birdsong structure. Often-
383 replicated results show that birds typically increase the spectral frequency and delivery rate of
384 their acoustic signals under a regime of more moderate anthropogenic noise (Patricelli &
385 Blickley 2006; Slabbekoorn & Den Boer-Visser 2006). One explanation for the increase in
386 song frequency parameters in birds exposed to noise is that it releases the acoustic signals
387 from masking by low-frequency anthropogenic noise. However, the decrease in song
388 maximum and peak frequency does not lead to masking release during aircraft movements. If
389 anything, by reducing the frequency of their songs closer to the frequency of maximum
390 power in the aircraft sound, they are increasing the masking effect. Additionally, the decrease
391 in spectral parameters in the songs of the chiffchaffs at airports is not a direct response to
392 noise exposure (Verzijden *et al.* 2010). Recordings were made in between aircraft
393 movements, when ambient sound levels were comparable to those at control sites. It is
394 possible that chiffchaffs do increase the frequency of their songs during aircraft movements,
395 but this was impossible to measure as the aircraft noise precluded spectral measurements in
396 our recordings (Verzijden *et al.* 2010; Brumm *et al.* 2017).

397

398 If the birds would respond to aircraft noise by singing louder (which we did not measure) as
399 predicted by the Lombard effect, we would expect an increase rather than a decrease in
400 frequency values (Nemeth *et al.* 2013). In addition, the level of aircraft noise close to the

401 airport runway is so high that the excitation patterns in the bird's cochlea, which is governed
402 by similar mechanisms as mammals (Saunders, Rintelmann & Bock 1979), will not produce
403 peaks that would allow detection of the signal in aircraft noise (Wong *et al.* 1998; Zilany *et*
404 *al.* 2009). Instead, the excitation pattern would become almost flat across a wide frequency
405 range, thus making it impossible to detect any additional signal that might be present at the
406 same time as the aircraft noise, i.e. aircraft noise will most likely lead to complete masking of
407 the signal (Zwicker 1970; Moore & Glasberg 1983; Wong *et al.* 1998; Zilany *et al.* 2009;
408 Moore 2012). This would mean that when close to an aircraft taking off, the birds would not
409 be able to perceive any other acoustic signal, irrespective of its spectral structure or
410 amplitude. In conclusion, the decrease in the maximum frequency of chiffchaffs' songs near
411 the airport is unlikely to be an adaptation to the local soundscape because it does not release
412 the song from masking by aircraft noise.

413

414 If it is not an adaptation to the local soundscape, then what may drive the spectral and
415 temporal changes in the songs of chiffchaffs near airports? Several other field studies
416 reported a decrease in spectral or temporal parameters in bird song. Red-winged blackbirds
417 (*Agelaius phoeniceus*) reduced the delivery rate (Ríos-Chelén, Lee & Patricelli 2015), while
418 great tits (*Parus major*) and white-crowned sparrows (*Zonotrichia leucophrys nuttalli*)
419 reduced the maximum frequency in their songs in response to noisy conditions (Halfwerk &
420 Slabbekoorn 2009; Gentry *et al.* 2017). The reduction in spectral characteristics was
421 explained as a strategy to increase the Signal-to-Noise ratio, either through masking release,
422 or through the concentration of energy in a narrower frequency bandwidth. However, these
423 strategies would not be effective at the airport. First, the energy in aircraft noise is biased
424 towards the low frequencies and thus a reduction in song frequency will not lead to effective
425 release from masking. Second, the soundscape at the airport between aircraft movements,

426 when the recordings were made, is similar to the soundscape of the control population. It is
427 therefore difficult to explain what selection pressure would drive the airport birds to use a
428 narrower frequency bandwidth, but not the birds in the control site.

429

430 A decrease in spectral parameters of songs has been observed in several laboratory studies
431 that involve birds with acquired hearing loss. The downward shift in song frequency (\pm
432 200Hz) observed in the current study is consistent with the effect observed in zebra finches
433 (*Taeniopygia guttata*) with acquired hearing loss due to long-term noise exposure (Potvin &
434 MacDougall-Shackleton 2015). Similarly, surgically deafened budgerigars (*Melopsittacus*
435 *undulatus*) and zebra and Bengalese finches (*Lonchura striata*) also sing songs containing
436 more low-frequency syllables and at a slower rate (Watanabe, Eda-Fujiwara & Kimura 2007;
437 Watanabe & Sakaguchi 2010) compared to before deafening. In addition, the minimum
438 frequencies in the songs of chiffchaffs exposed to aircraft noise did not change, which is
439 consistent with the song behaviour of birds with laboratory-induced hearing impairment.

440

441 Birds regularly exposed to noise levels of more than 93 dB(A) may suffer from auditory
442 threshold shifts (Ryals *et al.* 1999; Dooling & Popper 2007). Although noise events differ in
443 intensity between territories, depending on distance to the runway, flightpath and
444 topographical features (see Figure 2), airport chiffchaffs are exposed to a noise event on
445 average every 180s throughout the day. Chiffchaffs that were exposed to the highest sound
446 levels showed the lowest maximum frequency in their songs, while the control population
447 showed the more commonly observed positive relationship between sound level and song
448 frequency. One potential explanation for the findings of decreased frequency and temporal
449 parameters in the songs is that the chiffchaffs suffer from Noise Induced Hearing Loss
450 (NIHL).

451 The downward shift of the maximum frequency in the songs of chiffchaffs at the airport is a
452 result of the songs containing fewer high-frequency syllables. This suggests that the high-
453 frequency notes disappear from their repertoire through selective attrition, a process observed
454 in surgically deafened birds (Watanabe & Sakaguchi 2010). Loud noise exposure,
455 irrespective of frequency content (Yost 2013), has the greatest impact on high-frequency
456 hearing (Marler *et al.* 1973), because hair cells located basally in the cochlea, where detection
457 of high-frequency sounds occurs, are most susceptible to damage (Wang & Ren 2012). Birds
458 require auditory feedback of their own song to maintain the song's acoustic structure (Price
459 1979; Nordeen & Nordeen 1992; Woolley & Rubel 1997; Woolley & Rubel 2002) and when
460 unable to detect the higher frequencies in their own song, they stop producing them (Wright
461 *et al.* 2004; Watanabe & Sakaguchi 2010). Therefore, if chiffchaffs at the airport suffer from
462 reduced sensitivity to high frequencies, they may not be able to hear the higher frequency
463 syllables in their own songs and as a result no longer produce them.

464 Chiffchaffs exposed to aircraft noise responded more aggressively to simulated territorial
465 intrusions than control birds, similar to other species exposed to anthropogenic noise (Phillips
466 & Derryberry 2018). In general, urban birds tend to be more aggressive, but whether this is
467 due to noise or other urban factors is not clear (Davies & Sewall 2016). The current study
468 contributes to the notion that noise may be a prominent factor, since many other aspects of an
469 urban area are not present at an airport. Indeed, the higher levels of aggression may be the
470 direct result of higher stress levels as a result of intermittent aircraft noise exposure, as
471 observed for humans (Stansfeld & Matheson 2003) and birds (Burger 1981; Goudie & Jones
472 2004) near airports. Harlequin ducks showed increased aggression for 2 hours after a low
473 flying military aircraft passed by (Goudie & Jones 2004), while in the current study
474 chiffchaffs were exposed to aircraft movement on average every 180s.

475

476 The overall high agitation level of airport chiffchaffs may also occur because they are less
477 able to use acoustic information to assess the quality of intruders, due to intermittent noisy
478 conditions. Airport birds were particularly aggressive in response to the airport-type stimulus,
479 which they demonstrated by attacking the loudspeaker more when it played airport-type
480 stimuli than when it played control-type stimuli (Fig 5). One explanation for the higher
481 response to low frequency stimuli is that the airport birds are more sensitive to low
482 frequencies due to frequency dependent NIHL. The airport stimuli may be perceived as full
483 song stimuli, whilst the control stimuli, containing more high frequency notes, would only be
484 perceived partially (Linhart *et al.* 2013). However, all playback trials were conducted in
485 between aircraft movements in periods of relative quiet. Therefore, noise cannot have been a
486 direct factor contributing to the difference in response. Although our results show that airport
487 chiffchaffs are able to detect the stimuli, it is possible that as a result of NIHL, they lack the
488 ability to perceive the fine structure of the songs (Lohr, Wright & Dooling 2003). In many
489 bird species, the fine structure of song conveys information about the quality of the singer,
490 and determines the individual response of a challenged individual (Podos 1997; Ballentine,
491 Hyman & Nowicki 2004; de Kort *et al.* 2009b). The airport birds may not be able to assess
492 the relative quality of the simulated intruder on the basis of acoustic information, and may
493 have to resort to visual displays and physical attack rather than enter into a vocal duel as a
494 first line of defence of their territory.

495

496 In conclusion, we have shown that chiffchaffs lower the maximum frequency of their songs
497 and decrease song rate when exposed to aircraft noise, which is consistent with the effects
498 observed in laboratory hearing-impaired birds. We have also shown that airport birds are
499 more aggressive than control birds. This mirrors studies on humans showing that intermittent
500 and extreme noise exposure can lead to non-auditory psychological effects such as increased

501 stress levels and aggressive behaviour (Basner *et al.* 2014). Humans and wildlife do indeed
502 seem to suffer similar consequences from noise exposure (Shannon *et al.* 2016). These results
503 are timely and add fuel to the debate on the ecological costs of airport expansion around the
504 world.

505

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511

512 **Authors' Contributions**

513 The study was designed by ADW, HS and SRK. Fieldwork was conducted by AW and SRK,
514 with ADW and SRK processing the data. All authors contributed to writing the paper and all
515 authors gave final approval for publication.

516

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520 **Data accessibility**

521 Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3nd978g>
522 (JAE-Wolfenden- et-al-2019-Songanalysis and JAE-Wolfenden- et-al-2019-Playback)

523

525 **References**

- 526 Arroyo-Solís, A., Castillo, J.M., Figueroa, E., López-Sánchez, J.L. & Slabbekoorn, H. (2013)
 527 Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban
 528 birds. *Journal of Avian Biology*, **44**, 288-296.
- 529 Ballentine, B., Hyman, J. & Nowicki, S. (2004) Vocal Performance influences female responses to
 530 male bird song: an experimental test. *Behavioral Ecology*, **15**, 163-168.
- 531 Barber, J.R., Crooks, K.R. & Fristrup, K.M. (2010) The cost of chronic noise exposure for terrestrial
 532 organisms. *Trends in Ecology and Evolution*, **25**, 180-189.
- 533 Basner, M., Babisch, W., Davis, A., Brink, M., Clark, C., Janssen, S. & Stansfeld, S. (2014) Auditory and
 534 non-auditory effects of noise on health. *Lancet*, **383**, 1325-1332.
- 535 Brumm, H. (2004) The impact of environmental noise on song amplitude in a territorial bird. *Journal*
 536 *of Animal Ecology*, **73**, 434-440.
- 537 Brumm, H., Zollinger, S.A., Niemelä, P.T., Sprau, P. & Schielzeth, H. (2017) Measurement artefacts
 538 lead to false positives in the study of birdsong in noise. *Methods in Ecology and Evolution*, **8**,
 539 1617-1625.
- 540 Burger, J. (1981) Behavioural responses of herring gulls *Larus argentatus* to aircraft noise.
 541 *Environmental Pollution series A, Ecological*, **24**, 177-184.
- 542 Burleson, C.E. (2002) Estimated airplane noise levels in A-weighted decibels. (ed. U.S.D.o.T.F.A.
 543 Administration). Federal Aviation Administration.
- 544 Buxton, R.T., McKenna, M.F., Mennitt, D. & Fristrup, K. (2017) Noise pollution is pervasive in U.S.
 545 protected areas. *Science*, **356**, 531-533.
- 546 Catchpole, C.K. & Slater, P.J.B. (2003) *Birdsong: Biological Themes and Variations*. Cambridge
 547 University Press, Cambridge.
- 548 Davies, S. & Sewall, K.B. (2016) Agonistic urban birds: elevated territorial aggression of urban song
 549 sparrows is consistent within a breeding period. *Biol Lett*, **12**.
- 550 de Kort, S.R., Eldermire, E.R., Cramer, E.R. & Vehrencamp, S.L. (2009a) The deterrent effect of bird
 551 song in territory defense. *Behav Ecol*, **20**, 200-206.
- 552 de Kort, S.R., Eldermire, E.R., Valderrama, S., Botero, C.A. & Vehrencamp, S.L. (2009b) Trill
 553 consistency is an age-related assessment signal in banded wrens. *Proc Biol Sci*, **276**, 2315-
 554 2321.
- 555 Dominoni, D.M., Greif, S., Nemeth, E. & Brumm, H. (2016) Airport noise predicts song timing of
 556 European birds. *Ecol Evol*, **6**, 6151-6159.
- 557 Dooling, R.J. & Popper, A.N. (2007) The effects of Highway Noise on Birds. pp. 1-74. The California
 558 Department of Transportation, Sacramento.
- 559 Fuller, R.A., Warren, P.H. & Gaston, K.J. (2007) Daytime noise predicts nocturnal singing in urban
 560 robins. *Biol Lett*, **3**, 368-370.
- 561 Gentry, K.R., Derryberry, E.P., Danner, R.M., Danner, J.E. & Luther, D.A. (2017) Immediate signalling
 562 flexibility in response to experimental noise in urban, but not rural, white-crowned
 563 sparrows. *Ecosphere*, **8**, e01916.
- 564 Gil, D. & Gahr, M. (2002) The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol*
 565 *Evol*, **17**, 133-141.
- 566 Gil, D., Honarmand, M., Pascual, J., Perez-Mena, E. & Macias Garcia, C. (2014) Birds living near
 567 airports advance their dawn chorus and reduce overlap with aircraft noise. *Behavioral*
 568 *Ecology*, **26**, 435-443.
- 569 Gill, S.A., Job, J.R., Muyers, K., Naghshineh, K. & Vonhof, M.J. (2015) Toward a broader
 570 characterization of anthropogenic noise and its effects on wildlife. *Behavioral Ecology*, **26**,
 571 328-333.

572 Goudie, R.I. & Jones, I.L. (2004) Dose-response relationships of harlequin duck behaviour to noise
573 from low-level military jet over-flights in central Labrador. *Environmental Conservation*, **31**,
574 289-298.

575 Habib, J., Bayne, E.M. & Boutin, S. (2007) Chronic industrial noise affects pairing success and age
576 structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology*, **44**, 176-184.

577 Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., Ten Cate, C. & Slabbekoorn, H.
578 (2011a) Low-frequency songs lose their potency in noisy urban conditions. *Proceedings of*
579 *The National Academy of Sciences, USA*, **108**, 14549-14554.

580 Halfwerk, W., Holleman, L.J.M., Lessells, C.M. & Slabbekoorn, H. (2011b) Negative impacts of traffic
581 noise on avian reproductive success. *Journal of Applied Ecology*, **48**, 210-219.

582 Halfwerk, W. & Slabbekoorn, H. (2009) A behavioural mechanism explaining noise-dependent
583 frequency use in urban birdsong. *Animal Behaviour*, **78**, 1301-1307.

584 Huss, A., Spoerri, A., Egger, M., Roosli, M. & Swiss Natl Cohort Study, G. (2010) Aircraft Noise, Air
585 Pollution, and Mortality From Myocardial Infarction. *Epidemiology*, **21**, 829-836.

586 Kight, C.R. & Swaddle, J.P. (2011) How and why environmental noise impacts animals: an integrative,
587 mechanistic review. *Ecology Letters*, **14**, 1052-1061.

588 Linhart, P., Jaska, P., Petruskova, T., Petrusek, A. & Fuchs, R. (2013) Being angry, singing fast?
589 Signalling of aggressive motivation by syllable rate in a songbird with slow song. *Behavioural*
590 *Processes*, **100**, 139-145.

591 Linhart, P., Slabbekoorn, H. & Fuchs, R. (2012) The communicative significance of song frequency
592 and song length in territorial chiffchaffs. *Behavioral Ecology*, **23**, 1338-1347.

593 Lohr, B., Wright, T.F. & Dooling, R.J. (2003) Detection and discrimination of natural calls in masking
594 noise by birds: estimating the active space of a signal. *Animal Behaviour*, **65**, 763-777.

595 Marler, P., Konishi, M., Lutjen, N. & Waser, M.S. (1973) Effects of Continuous Noise on Avian Hearing
596 and Vocal Development. *Proceedings of The National Academy of Sciences, USA*, **70**, 1393-
597 1396.

598 Moore, B.C.J. (2012) *An Introduction to the Psychology of Hearing*, 6th edn. Brill, Leiden.

599 Moore, B.C.J. & Glasberg, B.G. (1983) Suggested formulae for calculating auditory-filter bandwidths
600 and excitation patterns. *The Journal of the acoustical Society of America*, **74**, 750-753.

601 Nemeth, E., Pieretti, N., Zollinger, S.A., Geberzahn, N., Partecke, J., Miranda, A.C. & Brumm, H.
602 (2013) Bird song and anthropogenic noise: vocal constraints may explain why birds sing
603 higher-frequency songs in cities. *Proc Biol Sci*, **280**, 20122798.

604 Nordeen, K.W. & Nordeen, E.J. (1992) Auditory Feedback Is Necessary for the Maintenance of
605 Stereotyped Song in Adult Zebra Finches. *Behavioral and Neurobiology*, **57**, 58-66.

606 Patricelli, G.L. & Blickley, J.L. (2006) Avian communication in urban noise: Causes and consequences
607 of vocal adjustment. *The Auk*, **123**, 639-649.

608 Phillips, J.N. & Derryberry, E.P. (2018) Urban sparrows respond to a sexually selected trait with
609 increased aggression in noise. *Sci Rep*, **8**, 7505.

610 Podos, J. (1997) A performance constraint on the evolution of trilled vocalizations in a songbird
611 family (Passeriformes: Emberizidae). *Evolution*, **51**, 537-551.

612 Podos, J. & Warren, P.S. (2007) The Evolution of Geographic Variation in Birdsong. *Advances in the*
613 *Study of Behavior*, **37**, 403-458.

614 Potvin, D.A. & MacDougall-Shackleton, S.A. (2015) Experimental chronic noise exposure affects adult
615 song in zebra finches. *Animal Behaviour*, **107**, 201-207.

616 Price, P.H. (1979) Developmental determinants of structure in zebra finch song. *Journal of*
617 *Comparative and Physiological Psychology*, **93**, 260-277.

618 Rich, E.L. & Romero, L.M. (2005) Exposure to chronic stress downregulates corticosterone responses
619 to acute stressors. *Am J Physiol Regul Integr Comp Physiol*, **288**, R1628-1636.

620 Ríos-Chelén, A.A., Lee, G.C. & Patricelli, G.L. (2015) Anthropogenic noise is associated with changes
621 in acoustic but not visual signals in red-winged blackbirds. *Behavioral Ecology and*
622 *Sociobiology*, **69**, 1139-1151.

- 623 Rodrigues, M. (1998) No relationship between territory size and the risk of cuckoldry in birds. *Animal*
624 *Behaviour*, **55**, 915-923.
- 625 Ryals, B.M., Dooling, R.J., Westbrook, E., Dent, M.L., MacKenzie, A. & Larsen, O.N. (1999) Avian
626 species differences in susceptibility to noise exposure. *Hearing Research*, **131**, 71-88.
- 627 Saunders, J.C., Rintelmann, W.F. & Bock, G.R. (1979) Frequency selectivity in bird and man: a
628 comparison among critical ratios, critical bands and psychophysical tuning curves. *Hearing*
629 *Research*, **1**, 303-323.
- 630 Shannon, G., McKenna, M.F., Angeloni, L.M., Crooks, K.R., Fristrup, K.M., Brown, E., Warner, K.A.,
631 Nelson, M.D., White, C., Briggs, J., McFarland, S. & Wittemyer, G. (2016) A synthesis of two
632 decades of research documenting the effects of noise on wildlife. *Biol Rev Camb Philos Soc*,
633 **91**, 982-1005.
- 634 Sierrro, J., Schloesing, E., Pavon, I. & Gil, D. (2017a) European blackbirds exposed to aircraft noise
635 advance their chorus, modify their song and spend more time singing. *Frontiers in Ecology*
636 *and Evolution*, **5**.
- 637 Sierrro, J., Schloesing, E., Pavón, I. & Gil, D. (2017b) European Blackbirds Exposed to Aircraft Noise
638 Advance Their Chorus, Modify Their Song and Spend More Time Singing. *Frontiers in Ecology*
639 *and Evolution*, **5**.
- 640 Slabbekoorn, H. (2013) Songs of the city: noise-dependent spectral plasticity in the acoustic
641 phenotype of urban birds. *Animal Behaviour*, **85**, 1089-1099.
- 642 Slabbekoorn, H. & Den Boer-Visser, A. (2006) Cities change the songs of birds. *Current Biology*, **16**,
643 2326-2331.
- 644 Slabbekoorn, H. & Peet, M. (2003) Birds sing at a higher pitch in Urban Noise. *Nature*, **424**, 267.
- 645 Stansfeld, S.A. & Matheson, M.P. (2003) Noise pollution: non-auditory effects on health. *British*
646 *Medical Bulletin*, **68**, 243-257.
- 647 Stansfeld, S.A. & Shipley, M. (2015) Noise sensitivity and future risk of illness and mortality. *Science*
648 *of the Total Environment*, **520**, 114-119.
- 649 Swaddle, J.P., Moseley, D.L., Hinders, M.K. & Smith, E.P. (2016) A sonic net excludes birds from an
650 airfield: implications for reducing bird strike and crop losses. *Ecological Applications*, **26**,
651 339-345.
- 652 Vehrencamp, S.L., Yantachka, J., Hall, M.L. & de Kort, S.R. (2013) Trill performance components vary
653 with age, season, and motivation in the banded wren. *Behav Ecol Sociobiol*, **67**, 409-419.
- 654 Verzijden, M.N., Ripmeester, E.A., Ohms, V.R., Snelderwaard, P. & Slabbekoorn, H. (2010) Immediate
655 spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. *J Exp*
656 *Biol*, **213**, 2575-2581.
- 657 Wang, Y. & Ren, C. (2012) Effects of repeated "benign" noise exposures in young CBA mice: shedding
658 light on age-related hearing loss. *J Assoc Res Otolaryngol*, **13**, 505-515.
- 659 Watanabe, A., Eda-Fujiwara, H. & Kimura, T. (2007) Auditory feedback is necessary for long-term
660 maintenance of high-frequency sound syllables in the song of adult male budgerigars
661 (*Melopsittacus undulatus*). *Journal of Comparative Physiology. A, Neuroethology, Sensory,*
662 *Neural and Behavioral Physiology*, **193**, 81-97.
- 663 Watanabe, A. & Sakaguchi, H. (2010) Comparative study of long-term reduction of high-frequency
664 song syllables in deafened zebra and Bengalese finches: implications for the role of auditory
665 feedback in song maintenance. *Journal of Ethology*, **28**, 491-505.
- 666 Wolfenden, A.D., Slabbekoorn, H.W., Kluk, K. & de Kort, S.R. (2019) Data from: Aircraft sound
667 exposure leads to song frequency decline and elevated aggression in wild chiffchaffs.
668 Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.3nd978g>
- 669 Wong, J.C., Miller, R.L., Calhoun, B.M. & Sachs, M.B.Y., E.D. (1998) Effects of high sound levels on
670 responses to the vowel /E/ in cat auditory nerve. *Hearing Research*, **123**, 61-77.
- 671 Woolley, S.M.N. & Rubel, E.W. (1997) Bengalese Finches *Lonchura striata domestica* depend on
672 auditory feedback for the maintenance of adult song. *Journal of Neuroscience*, **17**, 6380-
673 6390.

- 674 Woolley, S.M.N. & Rubel, E.W. (2002) Vocal Memory and Learning in Adult Bengalese Finches with
675 Regenerated Hair Cells. *Journal of Neuroscience*, **22**, 7774-7787.
- 676 Wright, T.F., Brittan-Powell, E.F., Dooling, R.J. & Mundinger, P.C. (2004) Sex-linked inheritance of
677 hearing and song in the Belgian Waterslager canary. *Proceedings of the Royal Society B-*
678 *Biological Sciences*, **271**, S409-S412.
- 679 Yost, W.A. (2013) *Fundamentals of hearing: An introduction*, 5th edn. Brill, Leiden.
- 680 Zilany, M.S., Bruce, I.C., Nelson, P.C. & Carney, L.H. (2009) A phenomenological model of the synapse
681 between the inner hair cell and auditory nerve: long-term adaptation with power-law
682 dynamics. *J Acoust Soc Am*, **126**, 2390-2412.
- 683 Zwicker, E. (1970) Masking and psychological excitation as consequences of the ear's frequency
684 analysis. *Frequency analysis and periodicity detection in hearing* (eds R. Plomp & G.F.
685 Smoorenburg), pp. 376-394. Sijthoff, Leiden.
- 686