

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32

Effects of signal features and background noise on distance cue discrimination by a songbird

Nina U. Pohl, Georg M. Klump, Ulrike Langemann

Cluster of Excellence "Hearing4all", Animal Physiology and Behaviour Group, Department
for Neuroscience, University of Oldenburg, Germany

Short title: distance cue discrimination

Word count: 6981 (excluding title page, summary, tables, references and figure captions)

Correspondence should be addressed to:

Ulrike Langemann

Cluster of Excellence "Hearing4all"

Animal Physiology and Behaviour Group

Department for Neuroscience

School of Medicine and Health Sciences

University of Oldenburg

D-26111 Oldenburg, Germany

Phone: xx49-441-798-3401

E-mail: ulrike.langemann@uni-oldenburg.de

33 **Abstract**

34 During the transmission of acoustic signals, the spectral and temporal properties of the
35 original signal are degraded and with increasing distance more and more echo patterns are
36 imposed. It is well known that these physical alterations provide useful cues to assess the
37 distance of a sound source. Previous studies in birds have shown that birds employ the degree
38 of degradation of a signal to estimate the distance of another singing male (referred to as
39 ranging). Little is known about how acoustic masking by background noise interferes with
40 ranging and whether the number of song elements and stimulus familiarity affect the ability to
41 discriminate between degraded and undegraded signals. In this study we trained great tits
42 (*Parus major* L.) to discriminate between signal variants in two background types, a silent
43 condition and a condition consisting of a natural dawn chorus. We manipulated great tit song
44 types to simulate patterns of reverberation and degradation equivalent to transmission
45 distances of between 5 and 160 m. The birds' responses were significantly affected by the
46 differences between the signal variants and by background type. In contrast, stimulus
47 familiarity or their element number had no significant effect on signal discrimination.
48 Although background type was a significant main effect with respect to the response
49 latencies, the great tits' overall performance in the noisy dawn chorus was similar to the
50 performance in silence.

51

52

53 **Key Words:**

54 acoustic communication, ranging, great tit, *Parus major* L.

55

56

57 **List of abbreviations**

58 SPL Sound-pressure level

59 GLMM general linear mixed model

60 ANOVA Analysis of variance

61

62 **Introduction**

63 Acoustic signals and acoustic communication is especially useful at long distances. Territorial
64 songbirds employ acoustic signals both for mate attraction and for defending a territory
65 (Collins, 2004). Degradation of the signals during transmission will provide the recipients
66 with cues revealing the distance of the sender, e.g., cues that reveal the position of a rival
67 male relative to the recipient's territory boundary. Assessing the distance of a sound source by
68 its physical properties is often referred to as ranging (Morton 1986). The major cues for
69 ranging are a change in overall amplitude of the signal, modifications of the signal envelope
70 with distance (e.g., by reverberations, Wiley and Richards, 1982), and a change of the signal's
71 frequency spectrum (e.g., by frequency-dependent attenuation, Marten and Marler 1977). All
72 of these cues have been shown to be useful to birds, although to a different extent, and for the
73 evaluation of some of these cues prior knowledge of the signal has been suggested to play a
74 role (Holland et al., 2001; Naguib et al., 2000).

75

76 Most evidence for distance perception and ranging in birds comes from field experiments.
77 Commonly conspecific song is played back from a loudspeaker to a territorial male and the
78 behaviour of the bird in response to these test signals is recorded. The signals are manipulated
79 to simulate different distances of a potential intruder. The experimental bird will usually
80 defend its territory and will approach the simulated intruder. From the flight distance relative
81 to the degree of degradation applied to the signal the experimenter can then infer the location
82 of the sound source perceived by the bird (Naguib and Wiley, 2001). In field experiments, the
83 effect of the subject's propensity to respond as well as its perceptual ability are difficult to
84 separate. Laboratory experiments can help not only to solve this dilemma by carefully
85 controlling the motivation of the subjects and response contingency, they can also
86 complement the knowledge obtained from the field. Laboratory studies on ranging in birds
87 investigated cues important for distance discrimination together with species identification
88 (Phillmore et al., 1998; Radziwon et al., 2011) or as a function of previous experience
89 (Phillmore et al., 2003). So far, however, little is known about how much the ubiquitous
90 background noise affects the perception of ranging cues in the natural environment (Brumm
91 and Naguib, 2009).

92

93 Here we employ trained wild birds to evaluate sets of signals representing various
94 transmission distances in order to compare the birds' sensitivity for ranging cues in two
95 different background types. The presence of background noise in the natural environment is

96 well known to impair signal detection and thus communication between animals of different
97 kind, which may ultimately impose fitness costs (Brumm, 2010; Laiolo, 2010; Read et al.,
98 2014). Commonly many birds, frogs or insects sing at the same time, and therefore mutually
99 mask their songs. Background noise produced by conspecifics and other vocalizing animals
100 will operate as an energetic masker if the masking background noise matches the frequency
101 spectrum of the signals. Conspecific vocalizations are especially potent maskers since they
102 match the spectro-temporal structure of a species' communication signals. Other substantial
103 masking effects are produced by wind moving the vegetation and by anthropogenic noise,
104 such as traffic noise (Brumm and Slabbekoorn, 2005). For these types of background noise, it
105 is mainly the signal-to-noise ratio at lower frequencies that interferes with long distance
106 communication (Langemann and Klump, 2005). Thus we decided to test the discrimination
107 ability of our experimental birds for distance cues both in a silent condition and in the
108 masking background noise of a natural dawn chorus. We also seek to understand how
109 previous experience affects the birds' ability to analyse such cues and whether the number of
110 signal elements affects the birds' assessment of ranging cues (as is known, for example, for
111 detection sensitivity, Swets et al. 1959).

112

113 Our study species was the great tit (*Parus major* L.), a common European songbird in which
114 males defend territories, and that has been shown to respond readily in ranging experiments,
115 both in the field (McGregor and Krebs, 1984) and in the laboratory (Langemann and Klump,
116 2005). In the present study, great tits obtained from the field were trained in the laboratory to
117 discriminate between great tit song elements that had been modified to simulate different
118 transmission distances. The test signals consisted of phrases (repeated units) that are naturally
119 found in great tit song and make up the different song types present in natural populations.
120 Sets of phrases from different song types were parametrically manipulated to show patterns of
121 reverberation and degradation equivalent to transmission distances of between 5 and 160 m
122 (here called virtual distances). These "echo patterns" were entirely computer generated and
123 were not obtained by simple re-recordings from songs broadcast in the field (which
124 commonly creates unwanted acoustic by-products). The method of signal generation we used
125 in the present study has been successfully applied in a field study (Naguib et al. 2000) in
126 which the approach behaviour of territorial chaffinches (*Fringilla coelebs* L.) was related to
127 the degree of degradation of the playback signals, demonstrating that the birds perceived
128 differences in degradation as differences in distance of a sound source.

129

130 Many species of songbirds sing different song types and it has been argued that experience
131 and thus stimulus familiarity might affect a bird's ability to assess the distance of a sound
132 source (Morton, 1998; Naguib, 1998; Wiley, 1998). Although the motivational context is very
133 different, when observing a bird in its natural or in the laboratory environment, both
134 approaches aim to estimate whether birds do make use of specific signal features. For
135 example, for assessing distance cues of a specific song type it is not necessary that a male
136 produces this song type itself, it is sufficient if it is heard from a neighbouring male
137 (McGregor and Avery 1986). Commonly, differences in the behavioural response to degraded
138 and non-degraded playback songs were found only if they were familiar to the focal male or if
139 they were very similar to the bird's own song, and little or no difference in response to
140 playback signals was found for unfamiliar signals (McGregor et al., 1983; Shy and Morton,
141 1986). A positive effect of stimulus familiarity on auditory processing has also been
142 demonstrated in a laboratory study (Seeba and Klump, 2009). The European starlings
143 (*Sturnus vulgaris* L.) were best to perceptually restore the "missing" parts of song signals
144 when they had prior experience with the signals compared to stimuli they were unfamiliar
145 with.

146
147 Patterns of reverberations together with the frequency-dependent attenuation are among the
148 cues that can be used for ranging. In the present study, we trained great tits to discriminate
149 between signals with echo patterns representing different virtual distances. We measured the
150 response latencies of the birds to estimate their discrimination ability. We predicted birds
151 would be better able to process distance cues for (1) large differences vs. small differences in
152 virtual distances between signals, (2) signals in the silent condition vs. the dawn chorus
153 condition, (3) signals with three vs. two elements, and (4) signals from familiar vs. unfamiliar
154 song types.

155

156

157 **Results**

158 In total, the six great tits performed 1075 experimental sessions. From these, 74 sessions were
159 not valid due to the false alarm rate exceeding the limit, in 129 sessions the rate of correct
160 responding was too low, and in a few cases the subject did not finish (8 sessions) or technical
161 dysfunction halted the session (5 sessions). When only valid sessions were taken into account,
162 the average false alarm rate was 6.2% and the average rate of correctly discriminating echo
163 variants from the reference was 52.8%. To estimate the birds' discrimination ability, we used
164 the individuals' response latencies from renditions of any possible reference-test combinations
165 of the echo variants (see Methods for details). The number of valid averages per bird was
166 between 240 and 360 (1890 altogether).

167
168 Neither total element duration nor the pause duration of different song types were associated
169 with the subjects' response latencies in a multiple regression analysis ($R^2 = 0.013$, $\beta = -0.117$,
170 $P = 0.27$ and $\beta = 0.116$, $P = 0.27$ for element duration and pause duration, respectively). We
171 thus included all song types into the analysis irrespective of element and pause duration. The
172 results of the GLMM ANOVA (Table 1) showed that the great tits' response latencies were
173 significantly affected by the background type in which the discrimination task was performed.
174 On average, response latencies were significantly longer in the dawn chorus condition (1483
175 ± 308 ms; mean \pm SD, here and throughout) compared to the silent condition ($1339 \pm$
176 326 ms). The birds' response latency was also significantly affected by the differences
177 between the virtual distances. Generally, large differences between echo patterns lead to short
178 response latencies while small differences lead to long response latencies (Figure 1). In
179 contrast to the first main effects, the order of presentation had only a minor effect on echo
180 discrimination. Response latencies to songs presented first in the silent and afterwards in the
181 dawn chorus condition were slightly longer (1420 ± 315 ms) compared to songs first
182 presented in the dawn chorus and then in the silent condition (1402 ± 335 ms). Neither the
183 familiarity of the song types nor their element number had a significant effect on response
184 latencies (Table 1). Bird identity had no effect either.

185
186 The GLMM ANOVA also revealed three significant interactions (Table 1). The strongest
187 interaction was found between background type and the order in which the test songs were
188 presented (Figure 2). Reaction times to test songs that were first presented in the silent
189 condition were on average rather similar. In contrast, reaction times to test songs first
190 presented in the dawn chorus condition were shorter in the silent condition than in the dawn

191 chorus condition. The next interaction was between stimulus familiarity and order of
192 presentation (Figure 3). Mean response latencies for discriminating familiar neighbouring
193 songs were on average shorter when they were presented first in the dawn chorus condition
194 compared to when they were first presented in the silent condition. In the case of the birds'
195 own song this difference was reduced, and it was reversed in the case of unfamiliar songs.
196 The least significant interaction was the one between background type and the differences
197 between the virtual distances.

198

199 The one-dimensional solutions of any of the PROXSCAL analyses explained more than 80%
200 of the dispersion's variance in each of the two background types. The perceptual space
201 coordinates of the different experimental classes as a function of the virtual distance are
202 shown in Figure 4. Similar perceptual space coordinates indicate that echo patterns from the
203 corresponding virtual distances have been perceived as being similar while larger differences
204 between coordinates indicate that the differences between these echo patterns were perceived
205 as being more salient. The perceptual distance values (i.e., space coordinates) varied
206 significantly with virtual distance in both background types (silent condition, $F=155.55$,
207 $P<0.001$; dawn chorus condition, $F=406.60$, $P<0.001$). Posthoc Tukey tests showed that,
208 within each of the two background types, all comparisons between virtual distances were
209 significantly different (all $P < 0.01$), except the comparisons between the two shortest (5m
210 and 10m) and the two longest (80m and 160m) virtual distances. Moreover, the perceptual
211 space coordinates determined in the silent condition and in the dawn chorus condition were
212 highly correlated for each of the experimental classes (R^2 values ranged from 0.74 to 0.99),
213 indicating similar relations between virtual distance and perceptual space coordinates in both
214 conditions.

215

216

217 **Discussion**

218

219 In this study we investigate how background noise interferes with the perception of distance
220 cues. Working under a controlled laboratory situation, we presented song signals in a realistic
221 masking situation to trained great tits by employing a natural dawn chorus recording. We used
222 variants of song signals with an increasing degree of degradation to test how stimulus
223 familiarity or the number of song elements affected the birds' ability to discriminate between
224 degraded and undegraded signals. Our results demonstrate that echo patterns simulating the
225 degradation of song signals for different transmission distances can be discriminated by the
226 birds. In the introduction we have made four predictions regarding the discrimination of echo
227 patterns that we are discussing below.

228

229 *Echoes indicate transmission distance*

230 Previous field experiments have proven the ranging ability of different bird species by
231 evoking territorial behaviour in response to conspecific playback song. A male will approach
232 the sound source in an attempt to localize its presumed rival and the distance covered and its
233 direction indicate the bird's ranging ability (Holland et al., 2001; Morton et al., 2006; Naguib
234 et al, 2000; Nelson and Stoddard, 1998). In addition, laboratory experiments allow
235 quantifying which of the different physical signal cues are behaviourally relevant for a bird
236 and which can be used at all. In the present study we used sets of signals differing in the
237 pattern of reverberation and degradation to simulate transmission distances of between 5 and
238 160 m. In accordance with our first prediction, the great tits indeed perceived echo patterns
239 from similar distances as being similar, while large differences in virtual distance were more
240 salient and therefore easier to discriminate. The outcome of the present study was comparable
241 to previous results from great tits (Langemann and Klump, 2005), but those experiments were
242 performed in the absence of any background noise. The interaction term between "virtual
243 distance" and "background type" has a very low F value and seems rather unimportant. Still, it
244 may indicate that distance cues are more readily available in the silent compared to the dawn
245 chorus condition, as seen in Figure 1: with increasing difference of virtual distance reaction
246 times drop slightly faster in the silent than in the dawn chorus condition.

247

248 For discriminating the different echo patterns, our great tits could rely on distance cues based
249 on reverberation patterns and frequency-dependent attenuation. Since we adjusted all echo
250 variants to the same rms amplitude, signal amplitude *per se* was not available as a cue.

251 Differences in overall amplitude have indeed been shown to be a possible cue for distance
252 assessment, both in laboratory studies (Phillmore et al., 1998; Radziwon et al., 2011) and in
253 the field (Naguib, 1997a; Nelson, 2000). Overall amplitude, however, is not a reliable
254 distance cue. Acoustic signals can be produced with different amplitude at the source already,
255 and movements of the singer's head will have an additional effect on signal amplitude (Larsen
256 and Dabelsteen, 1990; Nelson, 2000). It has been suggested that prior knowledge of the
257 signal's original spectrum at the sound source is required for employing the typical high-
258 frequency attenuation of signals as a ranging cue (Naguib and Wiley, 2001). Such a cue may
259 thus be especially useful for signals being familiar to the subject, as is the case, for example,
260 for songs used in the interaction between territorial neighbours. Reverberations added to a
261 signal during transmission should be a reliable distance cue, since the reverberation pattern
262 will inevitably change with distance. Most of the differences in the perceptual space
263 coordinates we see in Figure 4 resemble the gradual signal change in relation to increasing
264 virtual distance.

265

266 So far, only a few studies have tested the behavioural response of territorial birds for more
267 than two different degrees of degradation (Naguib et al., 2000; Nelson and Stoddard, 1998).
268 Chaffinches, for example (Naguib et al. 2000), showed a categorial response to playback of
269 degraded songs corresponding to transmission distances of between 0 and 120m, indicating
270 that the birds distinguished "short" (0, 20, and 40 m) from "long" distances (80 and 120 m). In
271 the context of territorial defence it might indeed be adaptive to initially differentiate between
272 only two categories, thus localizing potential threats either being "inside" or "outside" the
273 territory. Moreover a bird would most likely include visual information to narrow down the
274 location of another male. In perceptual terms, however, the present paper clearly shows that
275 great tits are well able to distinguish between acoustic signals coming from several distances.

276

277 *Echo discrimination in background noise*

278 In the wild, songbirds have to localize conspecifics in the ever present acoustic background
279 noise of their environment (Brumm and Slabbekoorn, 2005; Brumm and Naguib, 2009), with
280 the dawn chorus likely being one of the acoustically most challenging conditions. Therefore
281 we had our great tits perform the discrimination task in two conditions, i.e., with and without
282 background noise, but with the amplitude of the test signals fixed at the same value. We
283 predicted that echo discrimination in the dawn chorus condition should be impaired compared
284 to the silent condition. This was indeed the case. The response latencies of the great tits were

285 significantly longer in the dawn chorus condition compared to the silent condition (Figure 1).
286 These results are in line with previous studies showing that signal discrimination in
287 background noise deteriorates with decreasing signal-to-noise ratio (Lohr et al., 2003; Pohl et
288 al., 2012). Since the sound-pressure level of the test signals in our study was set well above
289 the great tits' masked auditory thresholds (Pohl et al., 2009), we can conclude that energetic
290 masking *per se* was not the main source for the difference in performance. Still, the noisy
291 background will interfere with the auditory input to some degree, such that soft parts of the
292 signals or the reverberation tails added to the signals may be affected. Thus the longer
293 response latencies in noise indicated that the physical differences between echo variants were
294 less salient and that the task might have been more demanding in noise compared to the silent
295 condition (Luce, 1986). The interaction term between "background type" and "order of
296 presentation" might at first seem inconsistent with this pattern: Great tits first performing the
297 task in silence had no advantage when later on performing the task in the dawn chorus
298 (indicating no effect of background type). However, when they were first challenged to work
299 in the dawn chorus, their performance for the same test songs was much better in silence,
300 indicates that performance in silence is less demanding for the birds having experienced the
301 more difficult task first. Apart from the difference in response latency, the scaling analysis
302 revealed hardly any difference in the discrimination performance between the silent and the
303 dawn chorus conditions (Figure 4). This indicates that great tits are extremely well adapted to
304 coping with natural ambient noise. A possible mechanism to outweigh the detrimental effects
305 imposed by the background noise would be "investing" more time in neuronal computation
306 for making the decision (for effects of computational load and attention in humans, Muller-
307 Gass and Schröger, 2007). Such mechanisms may also play a role in field playback
308 experiments and for perception in real world conditions.

309

310 ***Do more elements provide for better echo discrimination?***

311 A study by Holland et al. (1998) showed that the degree of degradation between the different
312 element types in the song of the wren (*Troglodytes troglodytes*) varied considerably and
313 resulted in an element-specific pattern of degradation. In that case, more types of song
314 elements likely offered several independent cues on the degree of degradation and, thus,
315 together could provide better distance cues. Contrary to our prediction, the great tits did not
316 benefit from an additional song element and discrimination performance was similar for
317 signals composed of two or of three elements. This is surprising, since more song elements
318 will at least support signal detection (Swets et al. 1959) and we expected that more elements

319 would also increase the probability for detecting the relevant distance cues. In comparison to
320 the wrens (Holland et al., 1998, 2001), which commonly sing many different repeated
321 elements, great tits use only few element types. They most often sing two-element and three-
322 element song types. While the two notes of the great tit two-element song types always differ
323 in their temporal and spectral properties, the three-element song types will frequently include
324 a repeat of one of the two notes. Following Swets and colleagues, any repeat should improve
325 the auditory system's sensitivity by the square root of the number of independent
326 observations. Contrary to that expectation, however, we do not find element number to
327 improve echo discrimination.

328

329 *Echo discrimination as a matter of familiarity*

330 A number of field studies have demonstrated that familiarity with a specific song type will
331 affect a male's ability to discriminate between degraded and undegraded playback songs and
332 the ability to assess the distance of a sound source (McGregor et al., 1983; Morton et al.,
333 2006; Naguib, 1998; Shy and Morton, 1986). However, there are also field studies that did not
334 find enhanced ranging ability for familiar song types (Wiley and Godard, 1996), and even
335 unfamiliar sounds can be effectively ranged (Naguib, 1997b). Similarly, black-capped
336 chickadees (*Poecile atricapillus*) reared in the laboratory and not having experienced adult
337 vocalization could discriminate between undegraded and degraded songs and calls as well as
338 birds taken from the wild into the laboratory experiment (Phillmore et al., 2003). In summary,
339 different studies either do or do not provide evidence for improved distance cue
340 discrimination with the familiarity of the signals. Our data that we obtained under controlled
341 laboratory conditions, might thus indicate that stimulus familiarity is not a solid factor for
342 assessing distances at all.

343

344 One possible reason why we did not find an effect of familiarity on echo discrimination might
345 relate to our experimental design in which the great tits were "learning" the unfamiliar song
346 types, thus "unfamiliar" became "familiar" in the course of the experiments. Using an
347 experimental procedure similar to the present study, Seeba and Klump (2009) demonstrated
348 that stimulus familiarity affected the ability of European starlings to perceptually restore parts
349 of song signals that were experimentally replaced by noise. In these experiments a rather
350 restricted set of previously unfamiliar stimuli were presented so many times that the starlings
351 could have learned every single stimulus, still the effect of stimulus familiarity remained
352 suggesting that such learning effects are not an important issue for our present experiments.

353 The significant interaction between "stimulus familiarity" and "order of presentation" also
354 may relate to the learning issue discussed above, i.e., in the demanding dawn chorus condition
355 the birds appear to acquire the capability for improving their analysis in the silent condition.
356 This seems to take the largest effect for the songs of previous neighbours that may still be
357 familiar to the birds. The mechanism underlying the transfer, however, is unknown.
358
359

360 **Methods**

361

362 ***Subjects***

363 Six adult male great tits (*Parus major* L.) were the subjects in our behavioural experiments.
364 One of these birds had previous experience in detecting tonal or noisy signal elements, the
365 other five birds were naive. These birds were mist netted prior to or after the breeding season
366 (as indicated by the construction of a nest) from a woodland population near Oldenburg,
367 Germany, in 2006 (one individual), 2007 (four individuals), and 2009 (one individual). They
368 were housed in individual cages of 80 x 40 x 40 cm³ in a common bird room with at least 14
369 light hours. In the home cages the birds had unrestricted access to water and were fed with a
370 diet mainly consisting of sunflower seeds, rolled oats and dried insects. Before the start of an
371 experimental session, the subjects were deprived of food for about one to four hours, so that
372 they were motivated to earn food during the experiments. Food rewards during experimental
373 sessions consisted of pieces of mealworms that are favourite food items. Each bird was tested
374 five days per week and once or twice a day. The care and treatment of the birds were
375 approved by the Landesamt für Verbraucherschutz und Lebensmittelsicherheit, Lower
376 Saxony, Germany. Catching permits were issued by Landkreis Ammerland and by
377 Vogelwarte Helgoland/Wilhelmshaven, Lower Saxony, Germany. At the end, after about a
378 year of experimental testing, the birds were released into the woods, at the place where we
379 had caught them.

380

381 ***Song recordings***

382 Great tit males from the study population were marked with individual combinations of
383 coloured plastic and an aluminium ring. We specifically recorded the song repertoire of
384 identified males and the repertoire of their neighbours. We also recorded singing activity from
385 non-ringed great tits to sample the song type repertoire of the field site. Recordings were
386 made between 7:00 and 14:00 MEZ from February until April in 2006, 2007, and 2009. To
387 obtain song types unknown to our study population, we recorded great tit males from
388 woodland and urban populations at least 7 km away from our field site. Songs were recorded
389 with a sampling rate of 22.05 kHz using Sennheiser ME88/K3N (Wedemark, Lower Saxony,
390 Germany) or Sennheiser ME67 unidirectional microphones with foam windshields and a
391 Marantz PMD670 digital recorder (Longford, Middlesex, UK).

392

393

394 ***Song analysis***

395 Great tits typically group a small number of song elements into phrases that are repeated
396 several times per song (Lambrechts 1996; Slabbekoorn and den Boer-Visser 2006). Different
397 song types are distinguished by characteristic temporal and spectral features of their phrases.
398 The song types found in our great tit population mostly had two or three elements per phrase.
399 We ignored song types with more than three elements per phrase since these were rarely sung
400 and recorded. We obtained 108, 324, and 354 two-element song types in 2006, 2007, and
401 2009, respectively, and we had 19, 60, and 72 three-element song types for analysis in 2006,
402 2007, and 2009, respectively.

403

404 We defined three levels of familiarity with respect to a tested male: (1) song types derived
405 from the bird's own song were certainly "familiar" to the bird, (2) "familiar" song types of
406 neighbouring birds that were dissimilar from the bird's own song, and (3) "unfamiliar" song
407 types that were not performed in the study population and therefore were dissimilar to both,
408 own and neighbouring song types.

409

410 Signal features were analysed using Avisoft SASLab Pro software (version 4.52; Avisoft
411 Bioacoustics, Berlin, Germany; analysis done by N.U.P.). Each year of recording was
412 analyzed separately. Generally, ten different phrases were measured for each song type,
413 however, in 27% of the cases fewer than ten phrases could be analyzed. These measures were
414 also used to evaluate the dissimilarity of song types described below. Phrases were selected
415 from different positions of a song bout, excluding the first phrase of any song that often
416 shows shorter element durations or slightly deviant features compared to the following
417 phrases (Lambrechts and Dhondt, 1987). Phrases suitable for measurements were chosen
418 based on the sonogram representation (Fourier transformation, 11.6 ms Hamming Window,
419 256 samples at 22.050 kHz sampling rate, temporal overlap between adjacent spectra
420 93.75%). Duration measurements were taken from the waveforms. Frequencies and
421 associated relative signal amplitudes were measured from the logarithmic power spectra of
422 the song elements (Table 2 and Figure 5 for all measures taken). Since some song elements
423 include sinusoidal frequency or amplitude modulations, low- and high-frequency side bands
424 from song elements were inspected to identify those elements.

425

426 To evaluate the dissimilarity of song types we analyzed the signal features extracted from the
427 different song types with a discriminant function (Method I) and hierarchical cluster analysis

428 (Method II). As a basic statistical assumption, song types from different field recordings were
429 treated as different song types (and only statistics would show whether song types were
430 indeed different or similar to each other). We verified the output of these analyses by a
431 common method of visual classification (Method III). In summary, two song types were
432 defined as being dissimilar if all three methods of analysis came to a congruent conclusion of
433 dissimilarity.

434
435 (**Method I**) A stepwise discriminant function analysis (inclusion based on Wilks' lambda with
436 F for inclusion of 3.84 and F for removal of 2.71) was applied to identify groups of song types
437 by means of the discriminant functions obtained from the measures of temporal and spectral
438 features of each song type (Garson 2012a). We used the first two discriminant functions and
439 the cross-validated classification tables to distinguish between song types that were similar or
440 dissimilar to each other. Regarding the two-element song types the first two discriminant
441 functions accounted for 78.0, 77.2 and 70.5% of the variance in 2006, 2007, and 2009,
442 respectively. Regarding the three-element song types the first two discriminant functions
443 accounted for 93.8, 71.6, and 67.8% of the variance in 2006, 2007, and 2009, respectively.
444 Variables that were included by the discriminant analysis were interpreted as being of high
445 importance for classifying the song types. Those parameters that were included in the
446 discriminant function analysis in each of the three years are listed in Table 3 and 4. Song
447 types were classified as being dissimilar if there was no overlap between the data points of the
448 scatter plot produced on the basis of the first two discriminant functions.

449
450 (**Method II**) The hierarchical cluster analysis estimated dissimilarity between objects (song
451 types) by distance measures (Garson 2012b) obtained using the temporal and spectral features
452 listed in Table 2. After computing squared Euclidean distance measures based on the z-
453 transformed variables, clusters were constructed based on the average linkage. We defined all
454 phrases that were linked in the first step of the clustering process as belonging to the same
455 song type. Song types not linked in this step were defined as being dissimilar.

456
457
458 (**Method III**) Since visual sonogram analyses are known to be quite robust (but see Jones et al.
459 2001), we compared the groups of song types obtained with the statistical methods with a
460 classification by sonograms. Sonograms were created using a Fourier transformation
461 (parameters as stated above, temporal overlap 87.5%). For the visual classification we used

462 (1) the order of high and low frequency elements within a phrase, (2) the peak frequency of
463 elements, (3) the frequency range and possible frequency modulation of song elements, and
464 (4) the duration of song elements and inter-element pauses (McGregor and Krebs, 1982).
465 Song types that appeared clearly different with respect to one of these features were classified
466 as being dissimilar.

467

468 *Test signals*

469 We selected song types that would allow testing whether discriminating between different
470 echo patterns was affected by both the familiarity of a song type and by the number of its
471 elements. When selecting the experimental stimuli, song types were chosen based on the
472 classification in the song analysis described above and with respect to the subjects' former
473 territorial neighbours in the wild. First, the bird's own songs were inspected, then song types
474 from its neighbours were selected in a way that they were most different from the own song.
475 Thereafter, unfamiliar song types were chosen to be as dissimilar as possible from all song
476 types of the study population sung in the year the experimental bird was removed from the
477 woods. Generally two song types were selected for each level of familiarity (Table 5), both
478 for two- and three element song types.

479

480 Test signals consisted of a single phrase of a specific song type and with a specific echo
481 pattern. Different echo variants were synthesized as follows: For each song type six to ten
482 phrases from recordings with a good signal-to-noise ratio were selected and the frequency and
483 amplitude contours of each song element were sampled every 1.451 ms (using Avisoft
484 SASLab Pro). The frequency and amplitude contours as well as the element and pause
485 durations of all phrases measured from a specific song type were then averaged to form a
486 "standard" of this song type. These standards were run through a computer simulated virtual
487 forest (programmed by G. Klump, Matlab, The Mathworks Inc., Natick, MA, USA) in order
488 to impose reverberation at the stimuli, equivalent to sound transmission distances of 5, 10, 20,
489 40, 80, and 160 m (we call these distances "virtual distances" throughout the paper). These
490 distance fit well to the territory size of many great tits at our study site. Details of the
491 procedure can be found elsewhere (Naguib et al. 2000). Briefly, the program simulated a two-
492 dimensional forest of 500 x 600 m with 12 000 tree trunks that, on average, were spaced 5 m
493 apart. "Loudspeakers" and "microphones" were virtually placed at random positions within
494 the forest to simulate the denoted distances. Broadcast signals were reflected once from each
495 tree, attenuating the sound by 10 dB in order to simulate loss of sound energy by absorption

496 and scattering of the sound wave. In addition, sound was attenuated according to the 6 dB
497 spherical loss rule as well as at 10 dB/100 m excess attenuation (Marten and Marler, 1977;
498 Morton, 1975). To simulate effects of frequency-dependent attenuation a 128 point FIR filter
499 was used to represent the excess attenuation found in deciduous forests (Marten and Marler,
500 1977). The different echo variants obtained for all test signals were adjusted to the same root
501 mean square (rms) amplitude and were presented in the behavioural experiments with a sound
502 pressure level (SPL) of 58.5 dB(C).

503

504 *Dawn chorus masker*

505 In order to study how echo discrimination was affected by background noise, test signals were
506 presented both in a "silent condition" and in a "dawn chorus condition" consisting of a
507 recording from natural dawn chorus. The dawn chorus was a sample of 4.6 min recorded in a
508 deciduous forest in the UK (Treswell Wood, Nottinghamshire; sample rate 44.1 kHz; Sony
509 DAT recorder TCD-D8, Sony Europe Ltd., Weybridge, UK; Sennheiser ME20 microphone,
510 Wedemark, Germany). We chose this recording as the masker because it was free of any great
511 tit vocalizations and of anthropogenic noise. Hanning ramps (10 ms) were imposed at the start
512 and the end of the sound file to obtain a loop file without sudden level changes. In the
513 experiment, the file was played as a continuous masker at a natural sound pressure level of
514 58.5 dB(C) SPL (equivalent continuous sound pressure level, Leq). Figure 6A depicts an
515 arbitrary 10 s example out of the dawn chorus waveform. Figure 6B shows the power
516 spectrum density of the complete 4.6 min masker file, i.e. the median, first and third quartiles,
517 and the minimum and maximum amplitude values occurring in the analysis frames. The
518 frequency spectra were calculated using a 100 ms frame size without overlap and without
519 weighting window. Due to the irregular pattern of the singing birds on the recording, the
520 spectral characteristics of the dawn chorus file and the signal-to-noise ratio in the
521 discrimination task were constantly changing during an experimental session. In the
522 experiments, the birds triggered the onset of the test stimulus playback themselves (see
523 Procedure of operant testing), thus providing a unique masking situation for any replicate
524 signal exposure.

525

526 *Experimental setup*

527 The great tits were moved from their home cages to the experimental cage using a small
528 transfer cage. The experimental cage (26 x 22 x 30 cm³) was located within a sound-
529 attenuating echo-reduced chamber (sound-absorbing foam by Illbruck GmbH, Leverkusen,

530 Germany; cutoff frequency 500 Hz, $\alpha > 0.99$; total attenuation: 48 dB at 500 Hz, > 57 dB for
531 frequencies ≥ 1 kHz). At the front of the cage two response keys (observation key, report key)
532 with light-emitting diodes (LEDs) were attached. Below the response keys an automatic
533 rotary food dispenser was placed. Test signals and dawn chorus masker were played from two
534 separate channels of the computer sound card (Sound Blaster PCI 512 16 bit, 44.1 kHz
535 sampling rate). They were independently adjusted in level by computer-controlled attenuators
536 (TDT PA4; Tucker-Davies Technologies, Alachua, FL, USA). Both channels were added in
537 the input stage of the amplifier (Yamaha A-520, Nippon Gakki, Japan) driving the speaker
538 (Canton Twin 700, 200-9000 Hz, ± 2.5 dB; Canton Elektronik GmbH & Co. KG, Weilrod,
539 Germany) that was mounted above the experimental cage. All behavioural protocols were
540 controlled by a Linux-operated microcomputer. The behaviour of the birds was video
541 monitored. Sound levels were calibrated at least once per day (Brüel & Kjær 2238 Mediator,
542 Nærum, Denmark) by placing a microphone (Brüel & Kjær 4188 microphone) at the bird's
543 usual head position.

544

545 ***Procedure of operant testing***

546 The great tits were trained in a Go/NoGo procedure to discriminate the test signals from a
547 repeated reference signal. The reference signal was one of the six echo variants of a test signal
548 and was repeated every 1.3s. The remaining five echo variants served as the test signals. In
549 one experimental session (of about 40 min) the bird had to complete a series of trials. Each
550 trial started with a peck by the bird at the observation key. After a random time interval of
551 between 2 to 10 s, the next peck at the observation key lead to the replacement of the repeated
552 reference signal by a test signal. The random presentation scheme is a suitable method to
553 prevent an animal "predicting" time periods with a high probability of test signals. If the bird
554 pecked the report key within 2000 ms after the onset of the test signal (Go response), this was
555 scored as a "hit", and a food reward was given with a probability of between 70 and 80%.
556 This reinforcement mode ensures high motivation and constant rates of responding. A feeder
557 light was always presented as a secondary reinforcement. If the subject did not report a test
558 signal within the given response time (NoGo response), this was scored as a "miss". To obtain
559 a measure of spontaneous responding (the false alarm rate), we employed "catch trials" during
560 which the reference signal was continued and no test signal was played. NoGo behaviour in a
561 catch trial was scored as "correct rejection". A Go response during a catch trial or during the
562 random time interval resulted in a black-out period of 5 to 30 s. In a Go/NoGo procedure a
563 proportion of 50% correct responses is significantly higher than the random performance

564 estimated by the false-alarm rate in our study. To prevent any training effect, the sequence of
565 presentation of the song types was randomized. Moreover, half of the song types (one of the
566 two from each level of familiarity, Table 5) were first presented in the silent condition and
567 thereafter in the dawn chorus condition, for the other half it was *vice versa*.

568

569 ***Measuring the discrimination ability***

570 To measure the birds' discrimination ability, we used principles of multidimensional scaling
571 procedures (Arabie et al. 1978). We recorded the birds' response latencies comparing all
572 possible reference-test combinations of the echo variants of a specific song type. Short
573 response latencies indicated salient differences whereas long response latencies indicated that
574 signals were perceived as being similar (Dooling and Okanoya, 1995). Any possible
575 combination was presented ten times, and the individuals' averaged response latencies from
576 these ten renditions were the unit of analysis. Since each song type was available with six
577 echo variants and each of them had to serve as the reference signal once, the birds had to
578 complete six sessions per song type. In one session (60 trials) test signals were presented in
579 randomized order and each test signal was compared ten times against the reference signal
580 selected for that session, resulting in a matrix of averaged response latencies. Response
581 matrices were obtained in a factorial design (2 background type x 2 element number x 2 order
582 of presentation x 3 familiarity of song type x 15 virtual distance). For "bird's own song", three
583 subjects had only one three-element song type, and one bird had no three-element song type,
584 resulting in different numbers of valid averages for the different birds. Because of time
585 limitation, one subject was not tested with its own song. If the subject failed to respond to the
586 test signal, the response latency was set to the maximum response time (2000 ms). Sessions
587 with a false alarm rate of more than 20% or with a total response rate to deviating test signals
588 of less than 33.3% were discarded and repeated at the end of the experiments.

589

590 ***Data analysis***

591 Since the duration of elements and pauses were quite different between song types, we
592 considered possible effects of element or pause duration on response latencies. We applied a
593 multiple regression analysis to investigate the association between the average response
594 latencies of the subjects and the total element (all elements of a phrase) and pause durations
595 (all pauses of a phrase) for each of the test songs.

596

597 We then explored the birds' ability to discriminate between echo patterns by means of a
598 general linear mixed model analysis of variance (GLMM ANOVA). The dependent variable
599 consisted of the birds' mean response latencies. Independent variables were the background
600 type (silent condition, dawn chorus condition), the level of familiarity of the song types (bird's
601 own song, songs of neighbouring birds, unfamiliar songs), the element number of the song
602 types (two element per phrase, three element per phrase), the order of presentation (first in
603 silence, first in dawn chorus), and the differences between all virtual distances (i.e., 5m, 10m,
604 15m, 20m, 30m, 35m, 40m, 60m, 70m, 75m, 80m, 120m, 140m, 150m, 155m). Bird identity
605 was included as a random variable to test for potential differences between individuals. In the
606 result table we provide all main effects, and from the two-way interactions we present only
607 those that turn out to be significant. We do not provide interactions higher than two-way since
608 higher-order interactions are generally rather difficult to interpret.

609
610 Furthermore the response matrices of the birds describing the response latencies were
611 analyzed using the PROXSCAL algorithm (Commaneur and Heiser, 1993). This produced
612 one-dimensional object spaces and provided a measure of perceived similarity between the
613 echo patterns. Generally, response latencies decrease when stimulus differences get more
614 salient. The proximity between the coordinates obtained within the perceptual space was then
615 inspected for significant differences by a 1-way ANOVA for each of the two background
616 types, with virtual distance (i.e., 5m, 10m, 20m, 40m, 80m, 160m) being the independent
617 variable. To compare the representation of virtual distances between background types, we
618 correlated the perceptual distance values (i.e., the space coordinates) determined in the silent
619 and in the dawn chorus condition for each of the song stimuli defined by the experimental
620 classes. The experimental stimulus classes are listed in Table 5, they are based on a
621 combination of the level of familiarity with the song type, the number of elements in the song
622 type and the order of presentation in the experiments. All statistical analyses were performed
623 using the software package SPSS 18 or 21 (SPSS Inc, Chicago, IL, USA).

624
625

626 **Author contribution and conflict of interest**

627 Experiments were designed by Georg Klump. Nina Pohl conducted or supervised data
628 collection. Data analysis and manuscript preparation were performed by all three authors. No
629 competing interests are declared.

630

631

632 **Acknowledgements**

633 Susanne Groß und Annika Horn participated in data collection. Rainer Beutelmann supported
634 our data analysis. The numerous comments of our anonymous reviewers were extremely
635 helpful to improve our paper - thanks to all of you!

636

637 **Funding**

638 This study was supported by the Deutsche Forschungsgemeinschaft (SFB TRR 31).

639

640

641 **References**

642

643 **Arabie, P., Carroll, J. D. and DeSarbo, W. S.** (1987). *Three-way multidimensional scaling*
 644 *and related techniques*. Newbury Park, CA: Sage.

645 **Brumm, H.** (2010). Anthropogenic noise: Implications for conservation. In *Encyclopedia of*
 646 *Animal Behavior* (eds M. D. Breed and J. Moore), Vol 1, pp. 89-93. Oxford: Academic
 647 Press.

648 **Brumm, H. and Slabbekoorn, H.** (2005). Acoustic communication in noise. *Adv. Study*
 649 *Behav.* **35**, 151-209.

650 **Brumm, H. and Naguib, M.** (2009) Environmental acoustics and the evolution of bird song.
 651 *Adv. Study Behav.* **40**, 1-33.

652 **Collins, S.** (2004). Vocal fighting and flirting: the functions of birdsong. In *Nature's music:*
 653 *the science of birdsong* (ed. P. Marler and H. Slabbekoorn), pp. 39-79. San Diego:
 654 Elsevier Academic Press.

655 **Commaneur, J. J. F. and Heiser W. J.** (1993). Mathematical derivations in the proximity
 656 scaling (PROXSCAL) of symmetric data matrices. Research Report No. RR 93-04,
 657 Department of Data Theory, University of Leiden.

658 **Dooling, R. J. and Okanoya, K.** (1995). Psychophysical methods for assessing perceptual
 659 categories. In *Methods in Comparative Psychoacoustics* (ed G. M. Klump, R. J. Dooling,
 660 R. R. Fay and W. C. Stebbins), pp. 307-318. Basel: Birkenhäuser.

661 **Garson, G. D.** (2012a). *Discriminant Function Analysis*. Asheboro, NC: Statistical
 662 Associates Publishers.

663 **Garson, G. D.** (2012b). *Cluster analysis*. Asheboro, NC: Statistical Associates Publishers.

664 **Holland, J., Dabelsteen, T., Pedersen, S. B. and Larsen, O. N.** (1998). Degradation of wren
 665 *Troglodytes troglodytes* song: Implications for information transfer and ranging. *J.*
 666 *Acoust. Soc. Am.* **103**, 2154-2166.

667 **Holland, J., Dabelsteen, T., Bjørn, C. P. and Pedersen, S. B.** (2001). The Location of
 668 ranging cues in wren song: Evidence from calibrated interactive playback experiments.
 669 *Behav.***138**, 189-206.

670 **Jones, A. E., ten Cate, C. and Bijleveld, C. C. J. H.** (2001). The interobserver reliability of
 671 scoring sonagrams by eye: a study on methods, illustrated on zebra finch songs. *Anim.*
 672 *Behav.* **62**, 791-801.

673 **Laiolo, P.** (2010). The emerging significance of bioacoustics in animal species conservation.
 674 *Biol. Conserv.*, **143**, 1635-1645.

- 675 **Lambrechts, M. M.** (1996). Organization of birdsong and constraints on performance. In
 676 *Ecology and Evolution of Acoustic Communication in Birds* (ed. D. E. Kroodsma and E.
 677 H. Miller), pp. 305-320. Ithaca NY: Cornell University Press.
- 678 **Lambrechts, M. M. and Dhondt, A. A.** (1987). Differences in singing performance between
 679 male great tits. *Ardea* **75**, 43-52.
- 680 **Langemann, U. and Klump, G. M.** (2005). Perception and acoustic communication
 681 networks. In *Animal Communication Networks* (ed. P. K. McGregor), pp. 451–480.
 682 Cambridge: Cambridge University Press.
- 683 **Larsen, O. N. and Dabelsteen, T.** (1990). Directionality of blackbird vocalization.
 684 Implications for vocal communication and its further study. *Ornis Scand.* **21**, 37-35.
- 685 **Lohr, B., Wright, T. F. and Dooling, R. J.** (2003). Detection and discrimination of natural
 686 calls in masking noise by birds: estimating the active space of a signal. *Anim. Behav.* **65**,
 687 763-777.
- 688 **Luce, R. D.** (1986). *Response times: their role in inferring elementary mental organization*
 689 (Vol. 8). New York: Oxford University Press.
- 690 **Marten, K. and Marler, P.** (1977). Sound-transmission and its significance for animal
 691 vocalization. I. Temperate habitats. *Behav. Ecol. Sociobiol.* **2**, 271–290.
- 692 **McGregor, P. K. and Krebs, J. R.** (1982). Song types in a population of the great tits (*Parus*
 693 *major*): Their distribution, abundance and acquisition by individuals. *Behaviour* **79**, 126-
 694 152.
- 695 **McGregor, P. K. and Krebs, J. R.** (1984). Sound degradation as a distance cue in great tit
 696 (*Parus major*) song. *Behav. Ecol. Sociobiol.* **16**, 49-56.
- 697 **McGregor, P. K. and Avery M. I.** (1986). The unsung songs of great tits (*Parus major*):
 698 learning neighbour's songs for discrimination. *Behav. Ecol. Sociobiol.* **18**, 311-316.
- 699 **McGregor, P. K., Krebs, J. R. and Ratcliffe, L. M.** (1983). The reaction of great tits (*Parus*
 700 *major*) to playback of degraded and undegraded songs: The effect of familiarity with the
 701 stimulus song type. *Auk* **100**, 898-906.
- 702 **Morton, E. S.** (1975). Ecological sources of selection on avian sounds. *Am. Nat.* **109**, 17-34.
- 703 **Morton, E.S.** (1986). Predictions from the ranging hypothesis for the evolution of long
 704 distance signals in birds. *Behaviour* **99**, 65-86.
- 705 **Morton, E. S.** (1998). Degradation and signal ranging in birds: memory matters. *Behav. Ecol.*
 706 *Sociobiol.* **42**, 135-137.
- 707 **Morton, E. S., Howlett, J., Kopysh, N. C. and Chiver, I.** (2006). Song ranging by
 708 incubating male Blue-headed Vireos: the importance of song representation in repertoires

- 709 and implications for song delivery patterns and local/foreign dialect discrimination. *J.*
710 *Field Ornithol.* **77**, 291-301.
- 711 **Muller-Gass, A. and Schröger, E.** (2007). Perceptual and cognitive task difficulty has
712 differential effects on auditory distraction. *Brain Res.* **1136**, 169-177.
- 713 **Naguib, M.** (1997a). Use of song amplitude for ranging in Carolina wrens, *Thryothorus*
714 *ludovicianus*. *Ethology* **103**, 723-731.
- 715 **Naguib, M.** (1997b). Ranging of songs in Carolina wrens: effects of familiarity with the song
716 type on use of different cues. *Behav. Ecol. Sociobiol.* **40**, 385-393; Erratum in *Behav.*
717 *Ecol. Sociobiol.* **41**, 203.
- 718 **Naguib, M.** (1998). Perception of degradation in acoustic signals and its implications for
719 ranging. *Behav. Ecol. Sociobiol.* **42**, 139-142.
- 720 **Naguib, M. and Wiley, R. H.** (2001). Estimating the distance to a source of sound:
721 mechanisms and adaptations for long-range communication. *Anim. Behav.* **62**, 825-837.
- 722 **Naguib, M., Klump, G. M., Hillmann, E., Griebmann, B. and Teige, T.** (2000).
723 Assessment of auditory distance in a territorial songbird: accurate feat or rule of thumb?
724 *Anim. Behav.* **59**, 715-721.
- 725 **Nelson, B. S.** (2000). Avian dependence on sound pressure level as an auditory distance cue.
726 *Anim. Behav.* **59**, 57-67.
- 727 **Nelson, B. S. and Stoddard, P. K.** (1998). Accuracy of auditory distance and azimuth
728 perception by a passerine bird in natural habitat. *Anim. Behav.* **56**, 467-477.
- 729 **Phillmore, L. S., Sturdy, C. B. and Weisman, R. G.** (2003). Does reduced social contact
730 affect discrimination of distance cues and individual vocalizations? *Anim. Behav.* **65**,
731 911-922.
- 732 **Phillmore, L. S., Sturdy, C. B., Ramsay, S. M. and Weisman, R. G.** (1998). Discrimination
733 of auditory distance cues by black-capped chickadees (*Poecile atricapillus*) and zebra
734 finches (*Taeniopygia guttata*). *J. Comp. Psychol.* **112**, 282-291.
- 735 **Pohl, N. U., Slabbekoorn, H., Klump, G. M. and Langemann, U.** (2009). Effects of signal
736 features and environmental noise on signal detection in the great tit, *Parus major*. *Anim.*
737 *Behav.*, **78**, 1293-1300.
- 738 **Pohl N. U., Leadbeater, E., Slabbekoorn, H., Klump, G. M. and Langemann, U.** (2012).
739 Great tits in urban noise benefit from high frequencies in song detection and
740 discrimination. *Anim. Behav.*, **83**, 711-721.

- 741 **Radziwon, K. E., Welch, T. E., Cone, J. P. and Dent, M. L.** (2011). Identification of
742 auditory distance cues by zebra finches (*Taeniopygia guttata*) and budgerigars
743 (*Melopsittacus undulatus*). *J. Acoust. Soc. Am.* **129**, 3384-3392.
- 744 **Read, J., Jones, G. and Radford, A. N.** (2014). Fitness costs as well as benefits are
745 important when considering responses to anthropogenic noise. *Behav. Ecol.*, **25**, 4-7.
- 746 **Seeba, F. and Klump, G. M.** (2009). Stimulus familiarity affects perceptual restoration in the
747 European starling (*Sturnus vulgaris*). *PLoS ONE* **4**, e5974.
- 748 **Shy, E. and Morton, E. S.** (1986). The role of distance, familiarity, and time of day in
749 Carolina wrens responses to conspecific songs. *Behav. Ecol. Sociobiol.* **19**, 393-400.
- 750 **Slabbekoorn, H. and den Boer-Visser, A.** (2006). Cities change the songs of birds. *Curr.*
751 *Biol.* **16**, 2326-2331.
- 752 **Swets, J. A., Shipley, E. F., McKey, M. J. and Green, D. M.** (1959). Multiple observations
753 of signals in noise. *J. Acoust. Soc. Am.* **31**, 514-521.
- 754 **Wiley R. H.** (1998). Ranging reconsidered. *Behav. Ecol. Sociobiol.* **42**, 143-146.
- 755 **Wiley, R. H. and Richards, D. G.** (1982). Adaptations for acoustic communication in birds:
756 sound transmission and signal detection. In *Evolution and ecology of acoustic*
757 *communication in birds, vol I.* (ed. D. E. Kroodsma and E.H. Miller), pp 131-181. New
758 York: Academic Press.
- 759 **Wiley, R. H., Godard, R.** (1996). Ranging of conspecifics by Kentucky warblers and its
760 implications for interactions of territorial males. *Behaviour* **133**, 81-102.
- 761
- 762

763 **Tables**

764 **Table 1:** Results of a GLMM ANOVA with the response latencies of six great tit subjects as
 765 the dependent variable. Shown are main effects and significant two-way interactions.

766

Source of variation	d.f.	F-value	P-value
Background type	1, 1848	234.446	< 0.001
Familiarity	2, 1850	0.592	0.553
Element number	1, 1848	0.098	0.755
Order of presentation	1, 1848	4.694	0.030
Virtual distance	14, 1848	165.056	< 0.001
Background type X Order of presentation	1, 1848	21.961	< 0.001
Background type X Virtual distance	14, 1848	1.990	0.015
Familiarity X Order of presentation	2, 1848	10.117	< 0.001

767

768

769 **Table 2:** Signal features measured for song type analysis. Duration was measured in seconds,
 770 frequency in Hertz, and amplitudes in decibel. In a two-element song type two elements and
 771 the inter-element pause were measured, in a three-element song type all three elements and
 772 two inter-element pauses were measured. The last six parameters in the list only apply to song
 773 elements exhibiting sinusoidal frequency or amplitude modulations.
 774

Signal feature	Abbreviation
Total phrase duration	Δt total
Pause duration	pause
Element duration	Δt E1 (E2, E3)
Start frequency *	f start
End frequency	f end
Peak frequency	peak f
Peak frequency amplitude	peak f A
Minimum frequency*	min f
Frequency bandwidth*	f bw
Total minimum frequency*	total min f
Total frequency bandwidth*	total f bw
Frequency of low-frequency side band	f LF
Amplitude of low-frequency side band	A LF
Centre frequency	CF
Centre frequency amplitude	CF A
Frequency of high-frequency side band	f HF
Amplitude of high-frequency side band	A HF

775 *10 dB below peak amplitude

776

777

778 **Table 3:**
 779 Variables from two-element song types that were included by the discriminant function
 780 analysis in all three years of recording. The variables were obtained from discriminant
 781 analyses performed separately for each of the three years. The list thus depicts not the
 782 complete collection of variables but the set of variables that were important in all three years.
 783

Element	Parameter
Element 1	Minimum frequency*
	Total minimum frequency*
	Frequency of low-frequency side band
	Centre frequency
	Frequency of high-frequency side band
	Amplitude of high-frequency side band
Element 2	Start frequency
	End frequency
	Minimum frequency*
	Total frequency bandwidth*
	Total minimum frequency*

784 *10 dB below peak amplitude

785

786

787 **Table 4:**
 788 Variables from three-element song types that were included by the discriminant function
 789 analysis in all three years of recording. The variables were obtained from discriminant
 790 analyses performed separately for each of the three years. The list thus depicts not the
 791 complete collection of variables but the set of variables that were important in all three years.
 792

Element	Parameter
Element 1	Duration
	End frequency
Pause 1	Duration
Element 2	End frequency
	Centre frequency
	Frequency of low-frequency side band
	Amplitude of low-frequency side band
Element 3	End frequency
	Total minimum frequency*
	Centre frequency
	Frequency of low-frequency side band
	Amplitude of low-frequency side band

793 *10 dB below peak amplitude

794

795

796 **Table 5:** The experimental stimulus classes presented to the birds were based on a
 797 combination of familiarity, song type, and background type. The level of stimulus familiarity
 798 was defined with respect to each individual male and the sequence of presentation was
 799 randomized for each bird. Song types contained either two or three elements per phrase. In
 800 addition, the order of presentation of the song types was systematically varied: Half of the
 801 song types were presented first in the silent (S) and then in the dawn chorus (D) condition, the
 802 other half were first presented in the dawn chorus condition and then in the silent condition
 803 (D-S).

804

	birds own song types (familiar)	neighbouring song types (familiar)	unfamiliar song types
2-element song types	S-D / D-S	S-D / D-S	S-D / D-S
3-element song types	S-D / D-S	S-D / D-S	S-D / D-S

805

806

807

808 **Figure Legends**

809 Figure 1: The experimental stimuli consisted of sets of songs showing patterns of
810 reverberation and degradation equivalent to transmission distances (or "virtual distances") of
811 between 5 and 160 m. The panels show mean response latencies (mean \pm SE) of the six birds
812 as a function of the difference in virtual distance. Since all echo variants for each virtual
813 distance served as the reference signal, the different panels depict results for comparisons of
814 the response for each of the virtual reference distance separately (i.e., re 5 m, re 10 m, re
815 20 m, re 40 m, re 80 m).

816

817 Figure 2: Bars indicate the response latencies of six birds (mean \pm SE) as a function of
818 background type (silent condition, dawn chorus condition) with order of presentation as the
819 parameter. Songs were presented either first in the silent condition and thereafter in the dawn
820 chorus condition or *vice versa*.

821

822 Figure 3: Bars indicate response latencies of six birds (mean \pm SE) as a function of stimulus
823 familiarity of the test songs (bird's own song, neighbouring song, unfamiliar song) with order
824 of presentation as the parameter. Songs were presented either first in the silent condition and
825 thereafter in the dawn chorus condition or *vice versa*.

826

827 Figure 4: One-dimensional space coordinates of the PROXSCAL scaling analyses as a
828 function of virtual distance (N=6 birds). The proximity of the data points in the object space
829 provides a measure of perceived dissimilarity between the different signal patterns. Different
830 lines represent the experimental classes described in Table 5. Experimental stimulus classes
831 were arranged in a 3x2x2 design, with level of familiarity (bird's own song, neighbouring
832 song, unfamiliar song), number of elements (2-element song types, 3-element song types) and
833 order of presentation (presented first in silence, first in dawn chorus) as the factors. Panel (A)
834 shows space coordinates in the silent condition, panel (B) in the dawn chorus condition. In
835 each of the panels, the line with open circles represents the mean values.

836

837 Figure 5: Signal description and signal analysis. Great tits group a small number of song
838 elements (here E1, E2) into phrases that are repeated several times per song. Although
839 duration measurements were taken from the waveforms, they are illustrated here on the
840 spectrogram of a two-element song type (panel A). Frequencies and associated relative signal
841 amplitudes were measured from the logarithmic power spectra of the song elements. Panel

842 (B) depicts a power spectrum from element E2 shown in the upper panel; the threshold for
843 some of the parameters was set 10 dB below the peak amplitude. See Table 2 for full list of
844 signal parameters, together with their abbreviation.

845

846 Figure 6: Description of the dawn chorus masker. Panel (A) displays a 10 s example of the
847 dawn chorus' waveform (total duration of the natural dawn chorus recording was 4.6 min).

848 Panel (B) shows the frequency spectrum. The three middle lines represent the median (bold)
849 of the power spectrum density and the first and third quartiles (dashed) while the upper and
850 lower lines in the graph give the minimum and maximum amplitude values, respectively.

851

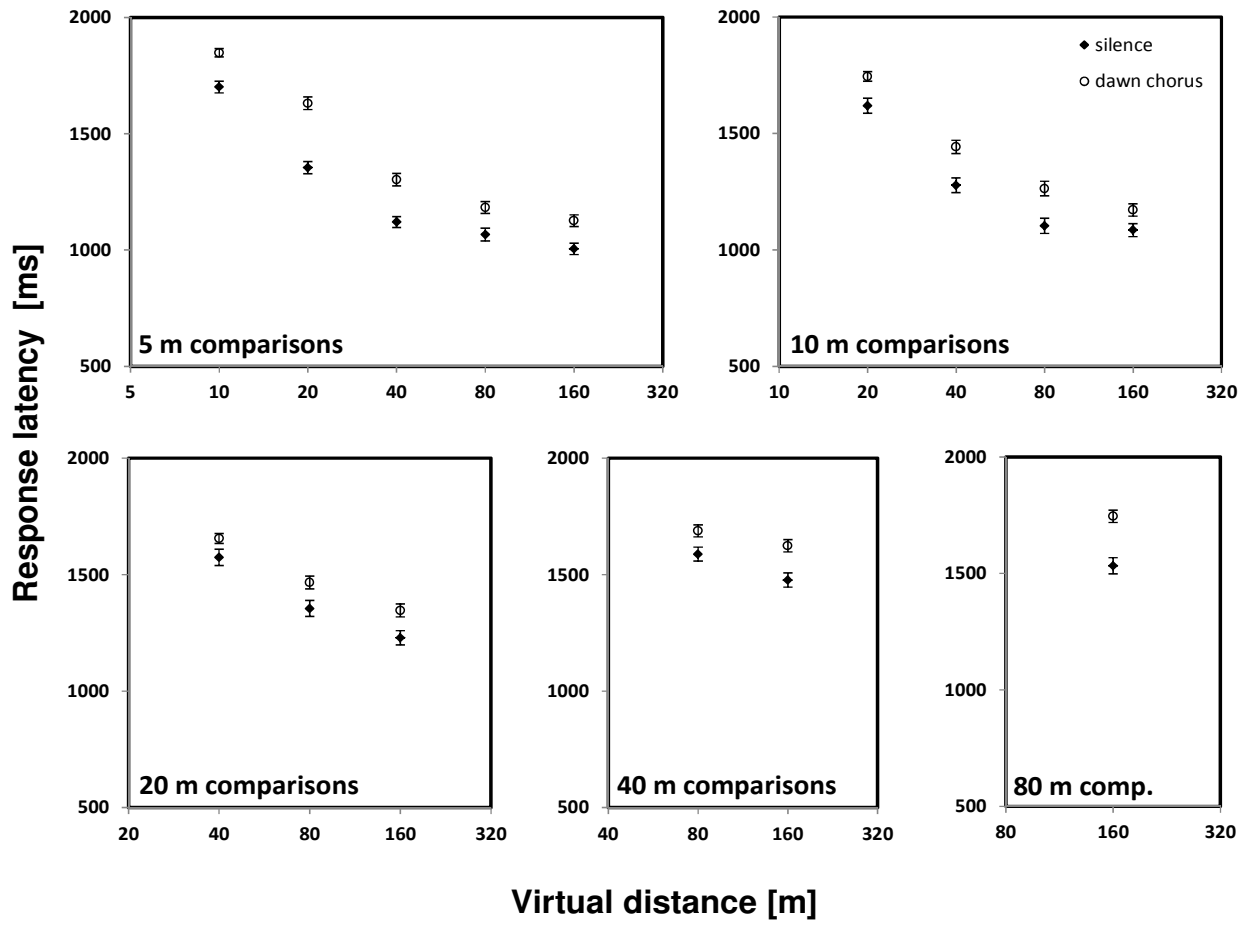


Figure 1

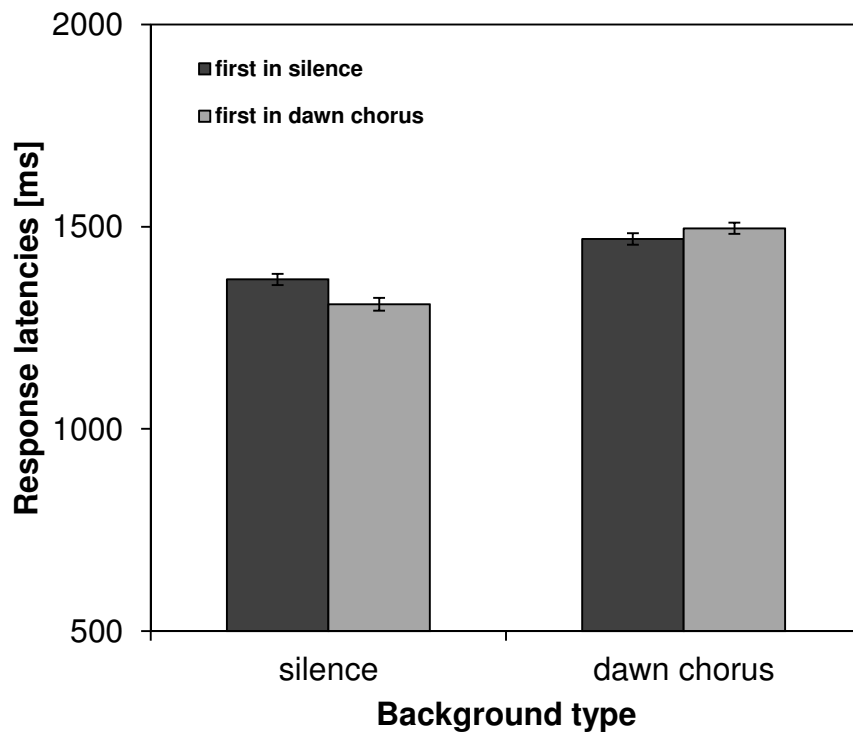


Figure 2

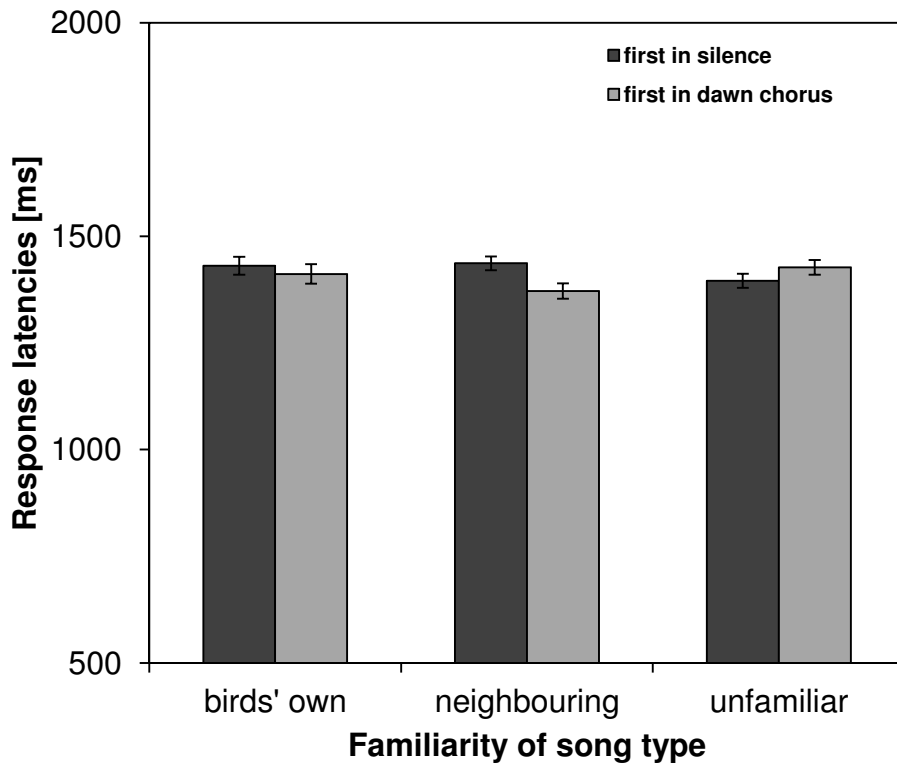


Figure 3

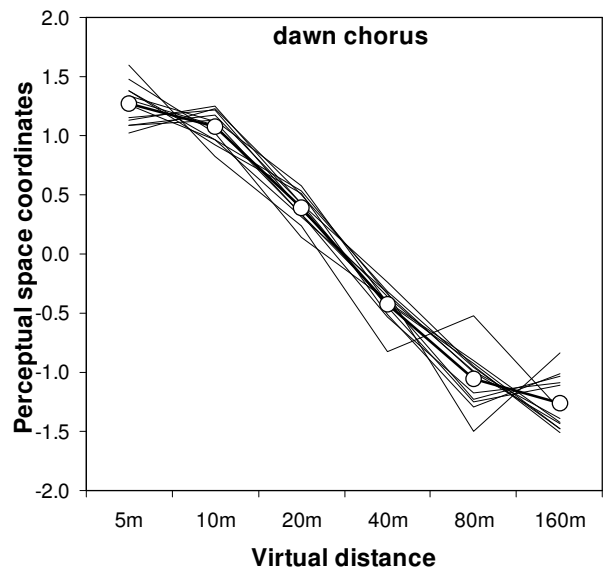
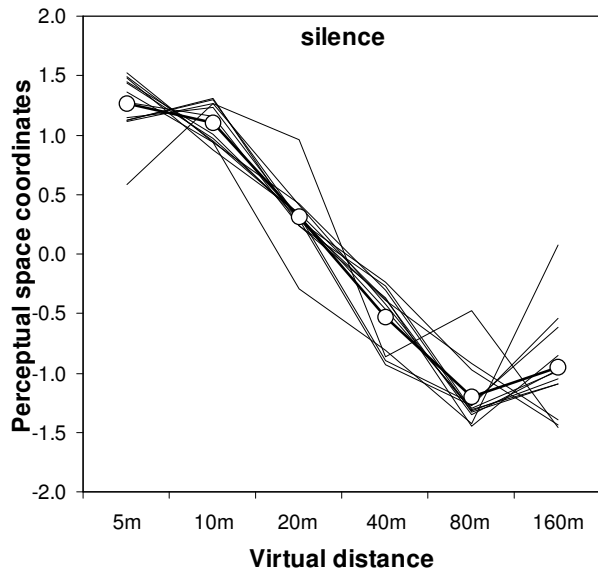


Figure 4

