



Disentangling Relations among Repertoire Size, Song Rate, Signal Redundancy and Ambient Noise Level in European Songbird

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Abstract

The majority of male songbirds have small repertoires and sing with eventual variety; that is, they present one song type several times before switching to the next one. Several hypotheses have been proposed to explain this phenomenon. The antiexhaustion hypothesis argues that song-type switching prevents muscle fatigue in the syrinx. The signal redundancy hypothesis suggests that repeating the same signal increases transmission success. Here, we have studied the song behaviour of the chaffinch, *Fringilla coelebs*, a common Eurasian species in which the males sing a few different song types and provide eventual variety. We tested different hypotheses to explain the temporal organisation of song output (repertoire size, song rate, bout duration, etc.) as a function of ambient noise by comparing birds from the same macrogeographic region in which the birds live either in a noisy town ($n = 71$) or in a quieter forest habitat ($n = 68$). Contrary to the prediction of the signal redundancy hypothesis and the results of earlier work on chaffinches living close to noisy streams, we found no significant differences in song characteristics between the town and forest populations. Our results support the antiexhaustion hypothesis because males with larger repertoires were able to sing with a significantly higher rate due to faster switching between different song types and producing shorter bouts. Sample size or population differences between our study and earlier investigations of the same species may explain the inconsistency with previous findings. Future studies should focus on determining the relations between song organisation and the directly measured quality of males and females' choice using, preferably, a longitudinal approach.

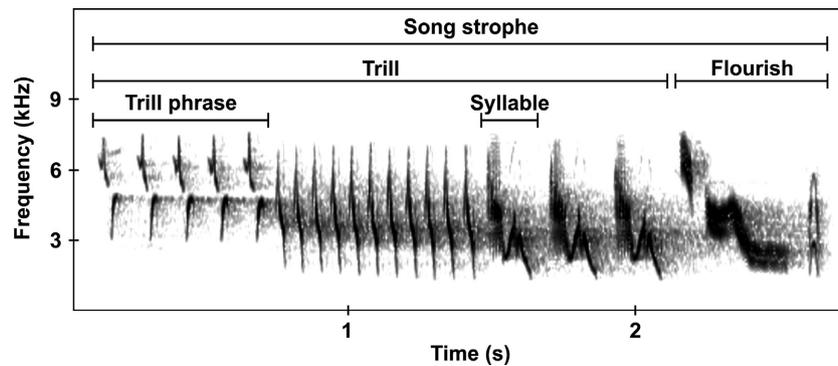
Introduction

Birds are some of the most vocal animals known. The sounds that birds produce are crucial for their interactions with other individuals. Their vocalisations are typically divided into calls and songs. Calls are often short signals that are used by both sexes in a relatively confined context (e.g. alarm calls are given when a potential predator is observed or begging calls are produced when nestlings demand a feeding). Songs tend to be longer and more complex. In temperate zones, songs are produced mostly by males during the breeding season. The primary functions of songs are

territorial defence and female attraction during the breeding season, but birds in the tropics often sing year-round, and both males and females may sing (Catchpole & Slater 2008; Odom et al. 2014).

Bird song is a complex phenomenon that has puzzled researchers for a long time. Birds can produce simple and short songs composed of only a few units called syllables (e.g. the great tit *Parus major*, McGregor & Krebs 1982; or the ortolan bunting *Emberiza hortulana*, Osiejuk et al. 2003) or utter long-lasting and very complex vocalisations (e.g. the eurasian skylark *Alauda arvensis*, Briefer et al. 2010; see Fig. 1 for illustrated definitions of all the song-related

Fig. 1: Spectrogram of a typical chaffinch song strophe. Syllable is a basic element of a song strophe. The trill section is usually composed of two or three trill phrases. Each trill phrase consists of repeated single syllable type. A much shorter flourish (ending phrase) is a sequence of different syllable type, and thus, flourish corresponds with motif term in more general bird song terminology.



terminology used). Some species, as the skylark noted above, can produce a continuous song with subsequent syllables that are more or less different from previous syllables. Other species have repertoires of one, a few or dozens of song types (different versions of their songs) and produce them with a repeatable pattern while singing (e.g. the great tit and ortolan bunting). Such a singing strategy may vary within and between species and between different contexts. Some male songbird species can sing with 'immediate' variety, which means that they switch between different song types after each song strophe (Fig. 1; Molles & Vehrencamp 1999). However, the majority of well-studied species sing with 'eventual' variety and produce several renditions of one song type (the so-called bout) before switching to another (Price 2013).

Despite much research, it is still unclear how repertoires evolved and why some songbirds choose to sing several renditions of a song type before switching to another. Larger repertoires are believed to be an indicator of male quality and females are observed to choose males producing larger repertoires over smaller ones (reviewed in Catchpole & Slater 2008; Price 2013). For example, some studies have revealed that repertoire size was positively correlated with fitness indicators such as survival probability or quality of nestlings (Macdougall-Shackleton et al. 2009; Grunst & Grunst 2014). In bird species with small- or medium-sized repertoires, the situation seems to be more complex. Here, the function of repertoire diversity is sometimes easier to understand by analysing how different song versions are used in communication (e.g. song-type matching, switching rate); the size of the repertoire plays a less important role. For example, in the song sparrow *Melospiza melodia*, the level of sharing song types with neighbours is more important for territory maintenance than for repertoire size (Hughes et al. 2007). Song-type switching may signal an increased level of aggressiveness (Kramer et al. 1985)

or reduce habituation by the receiver (the antihabituation/antimonotony hypothesis; Hartshorne 1956). Another explanation derives from the antiexhaustion hypothesis (Lambrechts & Dhondt 1988). This hypothesis argues that song repertoires evolved to prevent muscle fatigue in singing males. Long bouts of a particular song type may cause muscle exhaustion and may slow down the song rate. Song-type switching enables males to maintain a high song rate while repeating one particular song type before switching to another one. However, it seems logical that the lowest risk of muscle fatigue would occur when birds have large repertoires and sing with immediate variety. Species with large repertoires often sing with immediate variety (e.g. the European robin *Erithacus rubecula*; Brindley 1991). However, producing a large repertoire can be costly due to investment in a larger higher vocal centre of the brain (Airey et al. 2000), immune system suppression (Møller et al. 2000) or increased nutritional requirements (Nowicki et al. 2000). From the perspective of interspecific comparison, it is certain that many constraints define the mutual relations among song rate, repertoire size and the pattern of repertoire presentation.

Birds rely daily on their acoustic communication. It is crucial for birds to be heard by their addressed receivers so that the recipients perceive the signal well enough to decode specific information (Price 2013). Transmitted signals degrade over distance, and the degradation pattern depends on the characteristics of the environment. Additional factors such as high levels of background noise can have a strong negative impact on signal transmission (Barber et al. 2010), and repetition of a signal is suggested to make the signal more detectable (Wiley & Richards 1982). Therefore, singing with eventual variety may also be functionally linked to signal redundancy (i.e. repeating the same song type several times before switching to another type). It may be expected that birds singing under unfavourable conditions such high levels of

background noise will increase their song redundancy. One of the first indications of the use of increased signal redundancy derived from king penguins, *Aptenodytes patagonicus*, in which individuals increased their number of calls and number of syllables within calls during communication in noisy breeding habitats in Antarctica (Lengagne et al. 1999). A recent study revealed that male vermilion flycatchers *Pyrocephalus rubinus* living in noisy urban areas sang long songs and that males inhabiting quieter areas sang both short and long songs (Ríos-Chelén et al. 2013). Although these two studies provide interesting data, they do not concern songbirds (Oscines), in which song learning appears to have a strong influence on song development. Furthermore, songbirds may include those song types in their repertoires that have better acoustic transmission properties.

An example that songbirds can use signal redundancy comes from chaffinches *Fringilla coelebs*, a common Eurasian passerine bird. Chaffinches sing with eventual variety. Their song can be divided into two parts, a trill and a flourish (Fig. 1), providing the basis on which song types are classified. These birds can possess up to six different song types (Slater 1983). Brumm & Slater (2006) found that chaffinch males singing closer to noisy mountain streams tended to produce longer bouts of a particular song type before switching to another one. It seems that males are able to adjust their signal redundancy to an ambient noise level. In this study, though, the authors did not demonstrate whether the bout duration was also affected by other intrinsic song characteristics of males (e.g. repertoire size or song rate).

As the world becomes noisier due to human activity, many strategies to overcome high natural noise levels can be found in noisy urban areas (Slabbekoorn & den Boer-Visser 2006; Slabbekoorn 2013). If the increased signal redundancy in the song of the chaffinch was observed in natural noisy habitats, it seems likely that a similar strategy would be used in noisy urban areas.

In our study, we tested a few hypotheses to explain the temporal organisation of song output in relation to song repertoire size, song rate and ambient noise characteristics. In the first group of hypotheses, we investigated how singing characteristics change in habitats with different noise levels. We assumed that chaffinches exposed to anthropogenic noise behave in a similar way as chaffinches exposed to natural noisy habitats (Brumm & Slater 2006). Therefore, we predicted that chaffinches exposed to higher noise levels

would increase their bout duration and repeat the same song type more often before switching to another one compared with birds singing in a quieter, natural environment.

The second group of hypotheses refers to possible relations among repertoire size, song rate and bout duration. We hypothesised that a larger repertoire size would enable males to maintain higher song rates. We predicted that in such a case there would be a positive correlation between repertoire size and song rate. Because we linked the mechanism of maintaining a higher song rate with more frequent switching between different song types, we also predicted that males with larger repertoires would have shorter song bouts with fewer repetitions of a particular song type and shorter intervals between them. As we stated above, we supposed that noise level affected bout duration, but bout duration was also related to repertoire size. Therefore, we should observe the differences in singing patterns between habitats characterised by different ambient noise levels when modelling incorporates individual differences in repertoire size.

Material and Methods

Study Area and Population

Our study site was located in the Wielkopolska region in Western Poland. Recordings were conducted in parks and forests within an urban area of the city of Poznań (52°25.191' N, 16°55.795' E; 71 males recorded) and in forests surrounding the city to the north (Zielonka Forest Landscape Park, 52°33.183' N, 17°07.386' E; Noteć Forest, 52°43.530' N, 16°44.209' E; 68 males recorded). Sites were selected so that birds from similar habitats and belonging to a single dialect group could be recorded. According to our assumptions, the source of higher noise in urban areas was in proximity to streets. It was reasonable to expect that the potential differences in male song parameters would originate from sources such as individual variation (e.g. males' quality, social environment during song learning) or microscale differences between habitats (e.g. noise level), but not from macroscale differences (e.g. belonging to different dialect areas). Birds were recorded up to six hours after sunrise for three breeding seasons (2012–2014) from 15th March until 15th June. To exclude the possibility of recording a male more than once, each recording session (day) was conducted in a different location that was not visited again in the current year or following seasons.

We recorded the songs manually using a Marantz PMD670 recorder (Marantz Professional, Kanagawa, Japan) coupled with a Sennheiser ME67 shotgun microphone (Sennheiser, Wedemark, Germany) (123 males) and automatic Wildlife Acoustics SM2+ recorders (Wildlife Acoustics, Inc., Maynard, MA, USA) (16 males). All of the recordings were obtained at a monolinear PCM WAV with a 48-kHz sampling frequency and 16-bit resolution. All of the recordings were made during days with no rain and low wind speeds (<5 m/s). To define the wind speed, we used current weather forecast, and in the case of doubts, we measured the wind speed before the field recording with Voltcraft PL-130 anemometer. Chaffinches were found to increase their bout duration when a conspecific song was played back close to their territory (Riebel & Slater 2000). For this reason, observations were made while manually recording to check whether there were other singing males in close range to the recorded birds' territory. For recordings obtained with the SM2+ recorders, the placement of the recorders was chosen after an extended observation period of the focal male and his possible neighbours. After this observation period, the SM2+ units were placed in an area in the centre of frequently used song posts. Additionally, each recording made by the automatic recorder was analysed for other males singing in the background. Finally, for further analysis, we included only a single long series of continuous song from a single male from each SM2+ placement. The choice was based on song series continuity with the lack of amplitude differentiation, suggesting that the song post did not change.

We conducted noise-level measurements using a CHY 650 digital sound level meter (CHY Firemate Co., Ningbo, China) (range: 35–130 dB SPL re 20 μ Pa; frequency weighting: A; fast response; ANSI S1.4, Class II). Ten noise-level measurements were obtained after each manual recording and averaged for later data analysis. In the case of automatic recordings, we used the average value of the amplitude from the 10 measurements collected during the recorders' placement and after the recordings were finished.

Song Analysis

We used Avisoft SASlab Pro v. 5.2.x (Raimund Specht, Berlin, Germany) for the sound analysis. All of the measurements were taken from spectrograms with the following parameters: FFT length: 1024, frame size: 75%, window type: hamming, overlap: 75% (for a typical song, see Fig. 1). We analysed recordings in which the males sang at least 50

strophes. Sometimes chaffinches possess song types that they rarely use, but it is very unusual for males not to present their whole repertoire within the 50 continuous song strophes recorded (Slater et al. 1980; Böhner & Wistel-Wozniak 1995; Riebel & Slater 1999). To distinguish between different song types, we applied the methods of Slater & Ince (1979) and Slater et al. (1980). A song strophe was assigned to a particular song type if it had an identical syllable-type sequence in the trill part followed by a flourish (Fig. 1). For this purpose, we analysed 17,395 song strophes from 139 males ($\bar{x} \pm SD$: 139 ± 73.3 ; range: 54–469) to distinguish all of the song types used by the recorded birds.

The switch between bouts was defined by a transition to a different song type or a silent interval between songs strophes that was longer than 30 s (after Slater 1983). In practice, all analysed adjacent bouts consisted of different song types. For our statistical analysis of the song bout duration, we used subsample of 13,949 songs from the repertoires of 139 males ($\bar{x} \pm SD$: 100 ± 75.6 , range: 16–439 songs per male). In the subsample, we did not include the initial bout from each recording to avoid analysing incomplete bouts. For males who only sang a single song type (the so-called 'singleton males'), we analysed 1 176 songs strophes altogether ($\bar{x} \pm SD$: 53 ± 49.3 , range: 26–182 songs per male, $n = 22$). In all intervals between the songs used for analysis in singleton males, the intervals were shorter than 30 s (Slater 1983). For males with larger repertoires, we analysed 15 ± 14.8 bouts on average. We measured the number of song types, the number of songs in a bout, the bout duration (s), the song rate (strophes per min) and the song and between-song interval duration (s) for each male. All of the variables were averaged for each male.

Statistical Analysis

We applied generalised linear models (GLM) and linear regression (LR) for our modelling. For GLM (family Gaussian, identity link function), the predictor variables and covariates included year, day in a season, hour after sunrise, site, noise-level dB SPL, repertoire size of the focal male and the presence of other males within close range of the recorded male territory; we analysed these data to determine whether they influenced the log-transformed bout duration or the number of songs in a bout. In the case of LR, we used the backward stepwise method to remove the insignificant independent variables ($p < 0.05$). To verify which factors affected the song

rate, the number of songs in a bout and bout duration variables such as year, day in a season, hour after sunrise, site, noise-level dB SPL, repertoire size or the presence of other males within close range of the recorded male's territory were all used in the model. All of the means are presented with their accompanying SD, unless otherwise indicated. Prior to more advanced analyses, we tested the variables for normality using Kolmogorov–Smirnov one-sample test. All of the statistical analyses were two-tailed and were performed using STATA v. 13.1 (StataCorp, College Station, TX, USA) and IBM SPSS Statistics v. 22 (IBM Corp., Chicago, IL, USA).

Results

General Characteristics of Habitat Noise and Song Repertoires in the Studied Populations

Background noise differed markedly between the urban (51.4 ± 5.91 dB SPL, $n = 71$) and forest (40.1 ± 2.26 dB SPL, $n = 68$) sites (Mann–Whitney U -test = 75, $p < 0.001$, $n = 139$). The repertoire size of the recorded males ranged from 1 to 5 song types, with a mean of 2.24 ± 0.80 per male ($n = 139$). We classified 109 unique song types, 27 (25%) of which were shared by birds from both sites, 37 (34%) of which were found only in urban sites and 45 (41%) of which were found only in forest sites. For all of the recorded males, the song strophe duration ranged from 1.70 to 3.70 s with a mean of 2.51 ± 0.28 s. The intervals between song strophes ranged from 3.65 to 12.84 s with a mean of 6.86 ± 1.65 s. The song rate ranged from 4.82 to 13.38 songs per minute with a mean of 7.65 ± 1.54 songs ($n = 139$).

Differences in Song Characteristics between Habitats with Different Ambient Noise Levels

Site, increased noise levels and other parameters included in the model did not have a significant effect on the bout duration and the number of songs in a bout (Tables 1 and 2). We did not observe any significant differences in repertoire size (U -test = 2165.5, $p = 0.254$, $n = 139$), song rate (U -test = 2088, $p = 0.170$, $n = 139$), song strophe duration (U -test = 2119, $p = 0.214$, $n = 139$), intervals between song strophes (U -test = 1956, $p = 0.54$, $n = 139$), bout duration (U -test = 1672, $p = 0.844$, $n = 117$) or the number of songs in a bout (U -test = 1657, $p = 0.783$, $n = 117$) between the urban and forest sites. For the bout duration, data from the recordings of the singleton males were excluded from the analysis.

Table 1: Generalised linear model of site (urban vs. forest), males in background (present/absent), year, day in a season, hour after sunrise, noise level and repertoire size (2–5) on log-transformed bout duration on the basis of identity link function and Gaussian variance function (log likelihood = 51.258, AIC = -0.739 , BIC = -516.22 , $n = 117$, residual df = 109). Statistically significant values ($p < 0.05$) are in bold

Coefficients	Estimate	SE	Z value	p
Intercept	24.2715	56.152	0.43	0.666
Site (urban vs. forest)	-0.4918	0.048	-1.31	0.311
Males in background	-0.0373	0.034	-1.10	0.269
Year	-0.0108	0.028	-0.39	0.699
Day in a season	0.0002	0.001	0.24	0.810
Hour after sunrise	-0.0005	0.0111	-0.05	0.961
Noise level	-0.0031	0.0036	-0.86	0.392
Repertoire size	-0.2253	0.0238	-9.48	<0.001

Table 2: Generalised linear model of site (urban vs. forest), males in background (present/absent), year, day in a season, hour after sunrise, noise level and repertoire size (2–5) on log-transformed number of songs in a bout on the basis of identity link function and Gaussian variance function (log likelihood = 53.167, AIC = -0.772 , BIC = -516.32 , $n = 117$, residual df = 109). Statistically significant values ($p < 0.05$) are in bold

Coefficients	Estimate	SE	Z value	p
Intercept	21.9286	55.243	0.40	0.691
Site (urban vs. forest)	-0.0308	0.0478	-0.64	0.519
Males in background	-0.0260	0.0332	0.78	0.434
Year	-0.1015	0.0274	-0.37	0.711
Day in a season	-0.0005	0.0007	-0.70	0.487
Hour after sunrise	-0.0001	0.0109	-0.01	0.993
Noise level	-0.0005	0.0036	-0.13	0.894
Repertoire size	-0.1855	0.0234	-7.93	<0.001

Relations among Repertoire Size, Song Rate and Bout Duration

Repertoire size was significantly correlated with the mean song rate ($r_s = 0.51$, $p < 0.001$, $n = 139$; Fig. 2a). However, song rate, in contrast to song repertoire, is a rather flexible song characteristic that can be potentially affected by many factors. We used backward stepwise LR model to verify which possible confounding factors affected the song rate (Table 3). Our results revealed that only repertoire size and day of the season had a significant influence on song rate. As predicted, the song rate was higher when males had larger repertoires, and the song rate significantly decreased as the season progressed.

We also found that repertoire size was negatively correlated with the number of songs in a bout ($r_s = -0.57$, $p < 0.001$, $n = 117$; Fig. 2b), thereby affecting the bout duration ($r_s = -0.64$, $p < 0.001$, $n = 117$; Fig. 2c). The backward stepwise LR model

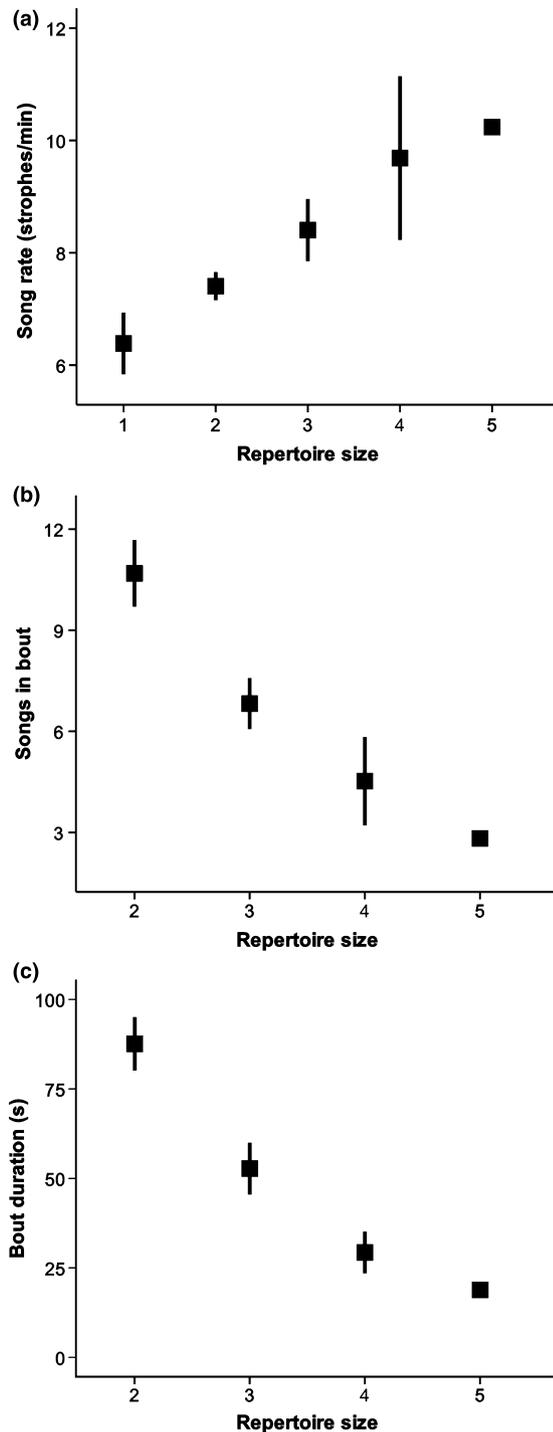


Fig. 2: Means and 95% CI of (a) song rate, (b) the number of song in a bout and (c) bout duration in chaffinch males with different repertoire size.

confirmed our prediction that repertoire size had a significant influence on the number of songs in a bout and a significant influence on the bout duration (Table 3).

Moreover, we found significant negative correlations between song rate and bout duration ($r_s = -0.44$, $p < 0.001$, $n = 117$, Fig. 3a), song strophe duration ($r_s = -0.38$, $p < 0.001$, $n = 139$, Fig. 3b) and the interval between song strophes ($r_s = -0.80$, $p < 0.001$, $n = 139$, Fig. 3c). Birds singing longer bouts produced song strophes less frequently ($r_s = -0.44$, $p < 0.001$, $n = 117$). We found no significant correlation between song rate and the number of songs in a bout ($r_s = -0.14$, $p = 0.137$, $n = 117$) and no significant effect of noise levels on the song rate ($r_s = 0.161$, $p = 0.058$, $n = 139$).

Discussion

We found that the noise level was significantly higher in the urban study site than in the forest study site. The chaffinches recorded in both areas shared many song types; as we expected, there was no sharp delineation between urban and forest populations in terms of general song characteristics. We did not find any significant differences in bout duration or the number of songs in a bout between noisy and quiet areas of urban and forest sites, or within the sites. Therefore, our results do not support the hypothesis that chaffinches increase signal redundancy when singing in environments with elevated noise levels.

In the first group of hypotheses, which were related to the impact of anthropogenic noise, we expected to find the differences in song characteristics between sites with different noise levels. Several studies have shown that some bird species change their song parameters, that is song rate (Montague et al. 2012) or song length (Ríos-Chelén et al. 2013; Lenske & La 2014), when singing in noisy conditions. However, our data do not support the predictions that chaffinches behave in a similar way when faced with anthropogenic noise. This observation may be due to a number of factors. First, there may be a high level of vocal plasticity between species; that is, some species increase their song duration (Francis et al. 2011; Ríos-Chelén et al. 2013) and other species shorten their song duration (Francis et al. 2011; McCarthy et al. 2013) when singing in noisy conditions. A third group of species does not modify their song duration when singing in noisy conditions (Gross et al. 2010; Hanna et al. 2011). Secondly, the acoustic parameters of songs can vary between conspecifics and the habitats they occupy (Slabbekoorn & Smith 2002). Habitat-dependent song divergence can shape responses to unfavourable conditions during acoustic communication over long-term adaptation to a particular habitat type. Furthermore, recent studies have shown that

Table 3: Results of backward stepwise linear regression with site (urban vs. forest), year, day in season, hour after sunrise, noise level (dB SPL), presence of males in background and repertoire size, entered into the model. The explained variables – song rate, the number of songs in a bout, bout duration – were log-transformed and had normal distribution after this transformation. Statistically significant values ($p < 0.05$) are in bold

Variables	Model	B	SE	Beta	t	p
Song rate	Intercept	0.812	0.024		33.276	<0.001
	Repertoire size	0.057	0.007	0.545	7.967	<0.001
	Day in a season	−0.001	<0.001	−0.256	−3.739	<0.001
Songs in bout	Intercept	1.362	0.057		23.83	<0.001
	Repertoire size	−0.183	0.022	−0.606	−8.165	<0.001
Bout duration	Intercept	2.366	0.058		40.824	<0.001
	Repertoire size	−0.226	0.023	−0.680	−9.954	<0.001

birds can respond differently to various types of natural and anthropogenic noise (Gough et al. 2014; Lenske & La 2014). Background noise can vary in temporal characteristics such as duration, frequency or intensity between and within natural and urban habitats and can affect the different aspects of acoustic communication (Luther & Gentry 2013). These studies have revealed that the relationship between noise and song parameters can be highly species specific and habitat specific.

Despite many different responses to noise that are possible, the vast majority of studies related to bird song parameters have focused on the changes in song frequency during exposure to noise (e.g. Slabbekoorn & den Boer-Visser 2006; Mendes et al. 2011; Redondo et al. 2013). Recent studies, however, have questioned the validity of the methods used for assessing frequency shifts (Zollinger et al. 2012; Nemeth et al. 2013; Ríos-Chelén et al. 2013). Moreover, shifted-frequency songs may not be as beneficial as once thought. For example, Luther & Magnotti (2014) studied the response of northern cardinal *Cardinalis cardinalis* males to songs with average and shifted (higher) minimum frequencies. Given low-amplitude background noise, males responded strongest to average-frequency songs. When the amplitude of noise was at the highest level, the response in both treatments was almost equal. Luther & Magnotti (2014) also noted that males adapted to singing high-pitched songs must be prepared to accept lower response rates in areas with less background noise. These findings and other recent studies cast doubts on the possible benefits of increasing song frequency and note a trade-off between song pitch and its signalling efficacy mediated by noise level (Slabbekoorn 2013; Read et al. 2014; Moiron et al. 2015).

Much clearer responses to elevated background noise have been found in studies that focused on singing effort (Cartwright et al. 2014) or song timing (Fuller et al. 2007; Arroyo-Solís et al. 2013; Lenske &

La 2014). This fact indicates that while background noise is a factor that masks acoustic signals, birds can adapt to such conditions. Birds were also found to vary in their response depending on the type of noise (Yang & Slabbekoorn 2014). Furthermore, anthropogenic noise is only one of the many consequences urban survivors have to face. Da Silva et al. (2014) showed that artificial light, rather than human-made noise, was responsible for the timing of dusk and dawn song bird choruses. Nevertheless, there is no doubt that urbanisation affects bird communities (e.g. Francis et al. 2009; Polak et al. 2013; Proppe et al. 2013; Sumasgutner et al. 2014).

Our findings yield new insights into the use of increased signal redundancy in communication under noisy conditions. Chaffinches recorded in urban and forest habitats of different background noise levels did not elongate their bout length by producing additional repetitions of strophes from particular song types. Our results contradict the findings of Brumm & Slater (2006); we note that these authors did not test whether repertoire size influenced bout duration, the number of songs in a bout or song rate. The mentioned relation was analysed later using a larger male sample; however, Brumm et al. (2009) were unable to explain the differences found in song rate between males. It is likely that the findings of both Brumm & Slater (2006) and Brumm et al. (2009) were influenced by geographical variation and the distance between the recorded males. Songs analysed in both studies were recorded at several sites in different council areas of Scotland. Recent data also show that bout duration can be used to attract females (Farrell et al. 2012) or in male–male interactions (Rivera-Cáceres et al. 2011). Consequently, associating bout length only with noise-related factors, as was described in the previous paragraph, can be misleading.

We did not observe any significant differences in song duration between urban and forest sites. Some species were found to repeat particular syllables or

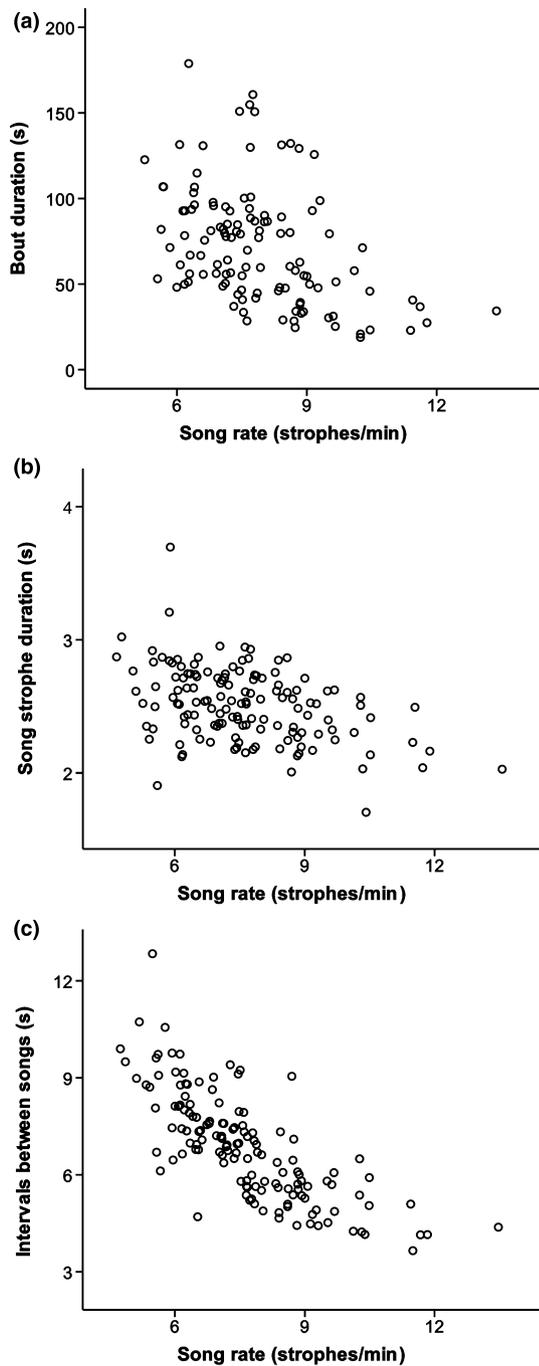


Fig. 3: Means and 95% CI of (a) bout duration, (b) song strophe duration (c) and interval between songs duration in relation to song rate measured as the average number of strophes per minute.

phrases in songs in a more redundant way when singing in noisy conditions (Hamao et al. 2011; Ríos-Chelén et al. 2013). Although this singing strategy was not directly tested in this study, we can assume that chaffinch males did not add extra syllables in their songs, because doing so would have increased

the song strophe duration. If males did add extra syllables, we would have found that the song duration differed between those sites that had different noise levels. We still cannot exclude the possibility that chaffinches sing in a more redundant way in cities by increasing their vocal activity as European serins *Serinus serinus* do (Díaz et al. 2011).

Although background noise did not impact song characteristics, we found significant differences in singing patterns between males. Male chaffinches with larger repertoires tended to sing at a faster rate and switch from one song type to another more often. The durations of their bouts were shorter, and they produced fewer songs per bout than birds singing fewer song types or singleton males. Our findings are consistent with the antiexhaustion hypothesis (Lambrechts & Dhondt 1988) and differ from the results of a previous study (with a comparable sample size) in which the antiexhaustion hypothesis was tested. Brumm et al. (2009) found no support for the antiexhaustion hypothesis in chaffinches. Another study in which the authors attempted to identify the mechanism that triggered the switch between different song types in chaffinches yielded ambiguous support for the antiexhaustion hypothesis (Riebel & Slater 1999). These authors found that song-type bouts with many repetitions were always delivered at a fast rate; short bouts were delivered either fast or slow. However, Riebel & Slater (1999) tested only six males whose repertoire sizes varied between two and three song types only.

Several hypotheses have been put forth to explain the origin and functions of repertoires in bird song. Our data indicate that song-type switching is important to maintain a high song production rate. A higher song rate can be advantageous when it comes to sexual selection because the fitness of the singing male is emphasised. Such an advantage can be especially beneficial for species that possess small repertoires. A faster song rate and switching from one song type to another more frequently allow singing males to present their full repertoire more quickly to a potential mate. Numerous studies have shown that repertoire size or a higher song production rate may indicate male quality (e.g. Bell et al. 2004; Kipper et al. 2006).

Our findings provide some support to the Beau Geste hypothesis in which Krebs (1977) suggested that repertoires can be used to defend territory. Dawson & Jenkins (1983) tested this hypothesis on chaffinches, and their results were contrary to the hypothesis predictions. Our data partially support the Beau Geste hypothesis. However, we did not focus on some key behaviours noted by Krebs (1977) (i.e.

coordinating flights between song posts, song-type switching and behaviour of rivals responding to such a singing strategy). Our results also revealed that the day in the season had a significant influence on this song rate (Table 2). This result supports earlier findings of Hanski & Laurila (1993). These authors noted that male chaffinches produced songs more intensively before pair formation and after losing a mate. These results suggest that the major function of song is female attraction and communication between paired birds.

In conclusion, we show that the measured attributes of chaffinch song characteristics did not differ between urban and forest habitats with different noise levels. However, some differences occurred in song-type sharing between those habitats that should be tested in future studies. We found that chaffinches exposed to anthropogenic noise did not behave in a similar way as chaffinches exposed to natural noisy habitats (Brumm & Slater 2006). This behaviour may be an effect of factors other than noise that influence singing. In our study, we provided clear evidence for relations between repertoire size and other song characteristics such as song rate, bout length and the number of songs in a bout. Males with larger repertoires were able to maintain a higher song production rate due to more frequent song switching, which supports the antiexhaustion hypothesis. The functionality of different song characteristics in chaffinches still does not remain fully understood despite the fact that the song of the species is relatively simple, the repertoire is small and birds of the species are common. To address this gap, we need to study this species by measuring song characteristics as well as by collecting data on male quality and female choice.

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Literature Cited

Airey, D. C., Buchanan, K. L., Szekely, T., Catchpole, C. K. & DeVoogd, T. J. 2000: Song, sexual selection and a

- song control nucleus (HVC) in the brains of European sedge warblers. *J. Neurobiol.* **44**, 1—6.
- Arroyo-Solís, A., Castillo, J. M., Figueroa, E., López-Sánchez, J. L. & Slabbekoorn, H. 2013: Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. *J. Avian Biol.* **44**, 288—296.
- Barber, J. R., Crooks, K. R. & Fristrup, K. M. 2010: The cost of chronic noise exposure for terrestrial organisms. *Trends Ecol. Evol.* **25**, 180—189.
- Bell, B. D., Borowiec, M., Lontkowski, J. & Pledger, S. 2004: Short records of marsh warbler (*Acrocephalus palustris*) song provide indices that correlate with nesting success. *J. Ornithol.* **145**, 8—15.
- Böhner, J. & Wistel-Wozniak, A. 1995: Chaffinch *Fringilla coelebs* song in western and southern Poland: song types, repertoire sizes, and the terminal element “kit”. *Acta Ornithol.* **30**, 107—115.
- Briefer, E., Osiejuk, T. S., Rybak, F. & Aubin, T. 2010: Are bird song complexity and song sharing shaped by habitat structure? An information theory and statistical approach. *J. Theor. Biol.* **262**, 151—164.
- Brindley, E. L. 1991: Response of European robins to playback of song: neighbor recognition and overlapping. *Anim. Behav.* **41**, 503—512.
- Brumm, H. & Slater, P. J. B. 2006: Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behav. Ecol. Sociobiol.* **60**, 475—481.
- Brumm, H., Lachlan, R. F., Riebel, K. & Slater, P. J. B. 2009: On the function of song type repertoires: testing the “antiexhaustion hypothesis” in chaffinches. *Anim. Behav.* **77**, 37—42.
- Cartwright, L. A., Taylor, D. R., Wilson, D. R. & Chow-Fraser, P. 2014: Urban noise affects song structure and daily patterns of song production in red-winged blackbirds (*Agelaius phoeniceus*). *Urban Ecosyst.* **17**, 561—572.
- Catchpole, C. K. & Slater, P. B. J. 2008: *Bird Song: Biological Themes and Variations*, 2nd edn. Cambridge Univ. Press, Cambridge, MA.
- Da Silva, A., Samplonius, J. M., Schlicht, E., Valcu, M. & Kempenaers, B. 2014: Artificial night light rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. *Behav. Ecol.* **25**, 1037—1047.
- Dawson, S. M. & Jenkins, P. F. 1983: Chaffinch song repertoires and the Beau Geste hypothesis. *Behaviour* **87**, 256—269.
- Díaz, M., Parra, A. & Gallardo, C. 2011: Serins respond to anthropogenic noise by increasing vocal activity. *Behav. Ecol.* **22**, 332—336.
- Farrell, T. M., Weaver, K., An, Y.-S. & MacDougall-Shackleton, S. A. 2012: Song bout length is indicative of spatial learning in European starlings. *Behav. Ecol.* **23**, 101—111.
- Francis, C. D., Ortega, C. P. & Cruz, A. 2009: Noise pollution changes avian communities and species interactions. *Curr. Biol.* **19**, 1415—1419.

- Francis, C. D., Ortega, C. P. & Cruz, A. 2011: Different behavioural responses to anthropogenic noise by two closely related passerine birds. *Biol. Lett.* **7**, 850—852.
- Fuller, R. A., Warren, P. H. & Gaston, K. J. 2007: Daytime noise predicts nocturnal singing in urban robins. *Biol. Lett.* **3**, 368—370.
- Gough, D. C., Mennill, D. J. & Nol, E. 2014: Singing seaside: Pacific wrens (*Troglodytes pacificus*) change their songs in the presence of natural and anthropogenic noise. *Wilson J. Ornithol.* **126**, 269—278.
- Gross, K., Pasinelli, G. & Kunc, H. P. 2010: Behavioral plasticity allows short-term adjustment to novel environment. *Am. Nat.* **176**, 456—464.
- Grunst, M. L. & Grunst, A. S. 2014: Song complexity, song rate and variation in the adrenocortical stress response in song sparrows (*Melospiza melodia*). *Gen. Comp. Endocrinol.* **200**, 67—76.
- Hamao, S., Watanabe, M. & Mori, Y. 2011: Urban noise and male density affect songs in the great tit *Parus major*. *Ethol. Ecol. Evol.* **23**, 111—119.
- Hanna, D., Blouin-Demers, G., Wilson, D. R. & Mennill, D. J. 2011: Anthropogenic noise affects song structure in red-winged blackbirds (*Agelaius phoeniceus*). *J. Exp. Biol.* **214**, 3549—3556.
- Hanski, I. K. & Laurila, A. 1993: Variation in song rate during the breeding cycle of the chaffinch, *Fringilla coelebs*. *Ethology* **93**, 161—169.
- Hartshorne, C. 1956: The monotony threshold in singing birds. *Auk* **83**, 176—192.
- Hughes, M., Anderson, R. C., Searcy, W. A., Bottensek, L. M. & Nowicki, S. 2007: Song type sharing and territory tenure in eastern song sparrows: implications for the evolution of song repertoires. *Anim. Behav.* **73**, 701—710.
- Kipper, S., Mundry, R., Sommer, C., Hultsch, H. & Todt, D. 2006: Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. *Anim. Behav.* **71**, 211—217.
- Kramer, H. G., Lemon, R. E. & Morris, M. J. 1985: Song switching and agonistic stimulation in the song sparrow (*Melospiza melodia*): five tests. *Anim. Behav.* **33**, 135—149.
- Krebs, J. R. 1977: The significance of song repertoires: the Beau Geste hypothesis. *Anim. Behav.* **25**, 475—478.
- Lambrechts, M. & Dhondt, A. 1988: The anti-exhaustion hypothesis: a new hypothesis to explain song performance and song switching in the great tit. *Anim. Behav.* **36**, 327—334.
- Lengagne, T., Aubin, T., Lauga, J. & Jouventin, P. 1999: How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proc. R. Soc. B* **266**, 1623—1628.
- Lenzke, A. K. & La, V. T. 2014: White-throated sparrows alter songs differentially in response to chorusing anuras and other background noise. *Behav. Process.* **105**, 28—35.
- Luther, D. & Gentry, K. 2013: Sources of background noise and their influence on vertebrate acoustic communication. *Behaviour* **150**, 1045—1068.
- Luther, D. & Magnotti, J. 2014: Can animals detect differences in vocalizations adjusted for anthropogenic noise? *Anim. Behav.* **92**, 111—116.
- Macdougall-Shackleton, S. A., Dindia, L., Newman, A. E. M., Potvin, D. A., Stewart, K. A. & Macdougall-Shackleton, E. A. 2009: Stress, song and survival in sparrows. *Biol. Lett.* **5**, 746—748.
- McCarthy, A. H., Potvin, D. A., Aslam, T., Bartlett, R., Beebe, S., Bennett, J., Hitchcock, D. J. & Tee, M. 2013: Differences between the songs of rural and urban Australian magpies (*Gymnorhina tibicen*) and the potential consequences for territorial interactions. *Notornis* **60**, 143—150.
- McGregor, P. K. & Krebs, J. R. 1982: Song types in a population of great tits (*Parus major*): their distribution, abundance and acquisition by individuals. *Behaviour* **79**, 126—152.
- Mendes, S., Colino-Rabanal, V. J. & Peris, S. J. 2011: Bird song variations along an urban gradient: the case of the European blackbird (*Turdus merula*). *Landscape Urban Plan.* **99**, 51—57.
- Moiron, M., González-Lagos, C., Slabbekoorn, H. & Sol, D. 2015: Singing in the city: high song frequencies are not guarantee for urban success in birds. *Behav. Ecol.* **26**, 843—850.
- Møller, A. P., Henry, P. Y. & Erritzøe, J. 2000: The evolution of song repertoires and immune defence in birds. *Proc. R. Soc. Lond. B* **267**, 165—169.
- Molles, L. E. & Vehrencamp, S. L. 1999: Repertoire size, repertoire overlap, and singing modes in the banded wren (*Thryothorus pleurostictus*). *Auk* **116**, 677—689.
- Montague, M. J., Danek-Gontard, M. & Kunc, H. P. 2012: Phenotypic plasticity affects the response of a sexually selected trait to anthropogenic noise. *Behav. Ecol.* **24**, 342—348.
- Nemeth, E., Pieretti, N., Zollinger, S. A., Geberzahn, N., Pertecke, J., Mirand, A. C. & Brumm, H. 2013: Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proc. R. Soc. B* **280**, 1—7.
- Nowicki, S., Hasselquist, D., Bensch, S. & Peters, S. 2000: Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. *Proc. R. Soc. Lond. B* **267**, 2419—2424.
- Odom, K. J., Hall, M. L., Riebel, K., Omland, K. E. & Langmore, N. E. 2014: Female song is widespread and ancestral in songbirds. *Nat. Commun.* **5**, 3379.
- Osiejuk, T. S., Ratyńska, K., Cygan, J. P. & Dale, S. 2003: Song structure and repertoire variation in ortolan

- bunting (*Emberiza hortulana* L.) from isolated Norwegian population. *Ann. Zool. Fennici* **40**, 3—16.
- Polak, M., Wiącek, J., Kucharczyk, M. & Orzechowski, R. 2013: The effect of road traffic on a breeding community of woodland birds. *Eur. J. For. Res.* **132**, 931—941.
- Price, J. J. 2013: Why is birdsong so repetitive? Signal detection and the evolution of avian singing modes. *Behaviour* **150**, 1—19.
- Proppe, D. S., Sturdy, C. B. & Clair, C. C. 2013: Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization. *Globa Chang Biol.* **19**, 1075—1084.
- Read, J., Jones, G. & Radford, A. N. 2014: Fitness costs as well as benefits are important when considering responses to anthropogenic noise. *Behav. Ecol.* **25**, 4—7.
- Redondo, P., Barrantes, G. & Sandoval, L. 2013: Urban noise influences vocalization structure in the house wren *Troglodytes aedon*. *Ibis* **155**, 621—625.
- Riebel, K. & Slater, P. J. B. 1999: Song type switching in the chaffinch, *Fringilla coelebs*: timing or counting? *Anim. Behav.* **57**, 655—661.
- Riebel, K. & Slater, P. J. B. 2000: Testing the flexibility of song type bout duration in the chaffinch, *Fringilla coelebs*. *Anim. Behav.* **59**, 1135—1142.
- Ríos-Chelén, A. A., Quirós-Guerrero, E., Gil, D. & Garcia, C. M. 2013: Dealing with urban noise: vermilion flycatchers sing longer song in noisier territories. *Behav. Ecol. Sociobiol.* **67**, 145—152.
- Rivera-Cáceres, K., Macías Garcia, C., Quirós-Guerrero, E. & Ríos-Chelén, A. A. 2011: An interactive playback experiment shows song bout size discrimination in the subsong vermilion flycatcher (*Pyrocephalus rubinus*). *Ethology* **117**, 1120—1127.
- Slabbekoorn, H. 2013: Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* **85**, 1089—1099.
- Slabbekoorn, H. & den Boer-Visser, A. 2006: Cities change the songs of birds. *Curr. Biol.* **16**, 2326—2331.
- Slabbekoorn, H. & Smith, T. B. 2002: Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. *Evolution* **56**, 1849—1858.
- Slater, P. J. B. 1983: Sequences of song in chaffinches. *Anim. Behav.* **31**, 272—281.
- Slater, P. J. B. & Ince, S. 1979: Cultural evolution in chaffinch song. *Behaviour* **71**, 146—166.
- Slater, P. J. B., Ince, S. & Cologan, P. 1980: Chaffinch song types – their frequencies in the population and distribution between repertoires of different individuals. *Behaviour* **75**, 207—218.
- Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H. W. & Gamauf, A. 2014: Hard times in the city – attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. *Front. Zool.* **11**, 48.
- Wiley, R. H. & Richards, D. G. 1982: Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic Communication in Birds*, Vol. **1** (Kroodsma, D. E., Miller, E. H., eds). Academic Press, New York, NY, pp. 132—181.
- Yang, X. J. & Slabbekoorn, H. 2014: Timing vocal behavior: lack of temporal overlap avoidance to fluctuating noise levels in singing Eurasian wrens. *Behav. Process.* **108**, 131—137.
- Zollinger, S. A., Podos, J., Nemeth, E., Goller, F. & Brumm, H. 2012: On the relationship between, and measurement of, amplitude and frequency in bird song. *Anim. Behav.* **84**, 1—9.