

The number of syllables per phrase in songs of Great Tits *Parus major* decreases with high levels of anthropogenic noise and at northern latitudes

Magne Husby^{1*} & Tore Slagsvold²

¹Section of Science, Nord University, Høgskoleveien 27, 7600 Levanger, Norway

²Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, N-0316 Oslo, Norway

* Correspondance, e-mail: magne.husby@nord.no

Cite this article

Husby M & Slagsvold T. 2023. The number of syllables per phrase in songs of Great Tits *Parus major* decreases with high levels of anthropogenic noise and at northern latitudes *Ornis Norvegica* 46: 28–42.
doi: 10.15845/on.v46.3854

Keywords

anthropogenic noise
bird communication
bird song
highway noise
latitude

Received 17 January 2023

Accepted 31 July 2023

Published 27 October 2023

Abstract

Birds often sing to defend a territory and to attract a mate. However, despite many studies, clear questions remain on how ecological conditions may affect the song, such as physical obstacles that may reduce the sound transmission, and anthropogenic noise that may mask the signal. The social environment of the local populations may also be important, such as breeding density and sex ratio, influencing the number of competing males with which to song match, and distances to neighbouring males and to prospecting females. During 2016–19, we counted the number of syllables (notes, elements) per phrase of singing male Great Tits *Parus major* by visiting seven countries in Europe and one country in North Africa. A total of 762 songs were observed by visiting 590 sampling points. We also recorded study year, levels of anthropogenic noise, calendar date, time of day, type of habitat and vegetation density, latitude, longitude and altitude. The most important explanatory variables for variation in songs were anthropogenic noise and the latitude of the sampling points; the number of syllables per phrase decreasing both with increasing levels of anthropogenic noise and with latitude. The latter result was also supported when listening to and analysing sonograms of Great Tits available at the Xenocanto repository for sound recordings, with fewer syllables per phrase for birds in Norway than in Spain and Portugal. We suggest that repetition of a short phrase is quickly interpreted by conspecifics in noisy environments, and that such signals are more readily detected by conspecifics over a wider area where the density of the birds is low.

INTRODUCTION

Birds often sing to defend a territory and to attract a mate but the fitness gains are reduced if the signal is masked or prevented from reaching the targeted receivers. How ecological conditions affect bird song has been widely studied, but some factors remain unclear and prominent questions still wait to be answered (Morton 1975, Brumm & Slabbekoorn 2005, Pohl et al. 2009, Halfwerk et al. 2011a). We still know little about the ecological contexts of signal modifications in animals (Berger-Tal et al. 2019). Various physical obstacles may reduce the transmission efficiency and quality of the song, including foliage of dense bushes and trees (Hunter & Krebs 1979, Blumenrath & Dabelsteen 2004, Lampe et al. 2007), and anthropogenic noise may mask the signal (Pohl et al. 2009, Pohl et al. 2012). The

social environment of the local populations may also be important, such as the local breeding density and sex ratio (Krebs et al. 1981), and the presence of competing species (Singh & Price 2015).

Background noise is possibly the most limiting acoustic property for bird song transmission (Brumm & Naguib 2009), and may hinder inter- and intra-specific communication (Pohl et al. 2012, Grade & Sieving 2016). Anthropogenic noise has been found to reduce territory quality of songbirds. For example, when comparing areas next to a busy highway with areas further away, Willow Warbler *Phylloscopus trochilus* males had longer breeding dispersal distances (Reijnen & Foppen 1991, Foppen & Reijnen 1994) and female Great Tits *Parus major* laid fewer eggs and produced fewer fledglings (Halfwerk et al. 2011b). However, noise may also improve breeding success because of

Table 1. The effects of noise on song characteristics in male Great Tits. The table includes studies where songs from urban, noisy areas were compared with songs from rural areas, and studies of songs when the background noise level was experimentally manipulated. + = increase, - = decrease, 0 = no change.

Song characteristics	Change	References
Song frequencies changed to differ from noise frequencies	+	Halfwerk & Slabbekoorn 2009, Huffeldt & Dabelsteen 2013
Minimum frequencies	+	Slabbekoorn & Peet 2003, Slabbekoorn & den Boer-Visser 2006, Salaberria & Gil 2010, Hamao et al. 2011, Kunc & Schmidt 2021
Mean and/or maximum frequencies	0	Slabbekoorn & den Boer-Visser 2006, Mockford & Marshall 2009, Salaberria & Gil 2010
	+	Bueno-Enciso et al. 2015
Frequency range	-	Slabbekoorn & Peet 2003, Salaberria & Gil 2010
Amplitude and territorial male response	+	Ritschard et al. 2012, Kunc & Schmidt 2021
Duration and inter-song intervals	-	Slabbekoorn & den Boer-Visser 2006, Mockford & Marshall 2009
	0	Akçay et al. 2020, Kunc & Schmidt 2021
Phrase length	0	Salaberria & Gil 2010
Song rate (songs per minute)	0	Bergen & Abs 1997, Akçay et al. 2020
Number of phrases per song and song length	+	Hamao et al. 2011
Number of syllables per phrase	0	Slabbekoorn & den Boer-Visser 2006

disruption of predator-prey interactions (Francis et al. 2009). The negative effects of anthropogenic noise may explain why birds are less abundant close to noisy roads than further away, both in forests (Reijnen & Foppen 1994; 1995, Reijnen et al. 1995, Goodwin & Shriver 2011) and in open landscapes (Reijnen et al. 1996, Stone 2000).

Often the frequencies of signals used in animal communication overlap with the frequencies of anthropogenic noise thereby decreasing the signal-to-noise ratio, although noise does not physically affect transmission patterns. Birds and other animals may respond to overlap by shifting frequency, amplitude and temporal structure so the information is less disturbed or masked to the receivers (Lombard 1911, Slabbekoorn & Peet 2003, Katti & Warren 2004, Warren et al. 2006, Brumm & Zollinger 2011, Halfwerk et al. 2011a, Dowling et al. 2012, Goodwin & Podos 2013, Colino-Rabanal et al. 2016). In noisy habitats, birds may also adjust the length and complexity of the song (Rios-Chelen et al. 2013).

Only a small number of the available acoustical cues are critical for species recognition (Emlen 1972), which can favor songs with only the most important information in noisy surroundings. From a study of

the songs of two species of *Phylloscopus* warblers, it was suggested that songs have evolved to be more complex in environments with few species, that is with less noise from other birds (Singh & Price 2015). Opposite to this result, two other *Phylloscopus* species did not change song characteristics in noise polluted areas, but instead with season and social factors (Deoniziak & Osiejuk 2019). The song of the Song Thrush *Turdus philomelos* was more complex in urban than in less noisy natural forests (Deoniziak & Osiejuk 2019). Further, Chaffinches *Fringilla coelebs* sang longer bouts of the same song type before switching to another type in areas with natural noise than in more silent surroundings (Brumm & Slater 2006), but not so in noisy urban environments (Deoniziak & Osiejuk 2016).

It has also been proposed that song length may reflect a trade-off between energetic costs versus song amplitude and length (Fernández-Juricic et al. 2005). Long songs may have an increased probability of detection because parts of the signal may be heard during silent windows of the noise (Brumm & Slabbekoorn 2005). There is not necessarily a relationship between the length of a song and the number of syllables (or notes and elements) per phrase because a short phrase can be repeated several times

and produce a long song. In noisy areas, a reduction in the number of syllables per song was found in the House Finch *Haemorrhous mexicanus* (Fernández-Juricic et al. 2005), and fewer introductory syllables or total number of syllables per song were reported in the Red-winged Blackbird *Agelaius phoeniceus* (Cartwright et al. 2014, Rios-Chelen et al. 2015). However, in the Winter Wren *Troglodytes troglodytes*, each syllable was longer in noisy areas (Colino-Rabanal et al. 2016). Another study of the House Finch found no association between song length and noise levels (Bermúdez-Cuamatzin et al. 2009). Moreover, the Pale-breasted Thrush *Turdus leucomelas* adjusted some features of the song in noisy areas, but not the average duration of each syllable (Mendes et al. 2017). A playback experiment gave no reliable evidence of noise-induced song flexibility in the Vermilion Flycatcher *Pyrocephalus obscurus* (Rios-Chelen et al. 2018).

Published findings do not seem to be consistent across the studies or the species of birds. However, the results show that birds in noisy areas may be able to adjust several features in their singing, including variation in the number of syllables, which indicates that noise adjustments of the number of syllables per phrase may be found in Great Tit songs. In Great Tits, most studies on song modification have examined the effects of urban noise on song frequency and amplitude and less is known about the temporal changes in the song pattern of a species (Table 1).

In the present study, we focused on the number of syllables per phrase in the Great Tit song in relation to anthropogenic noise and other environmental factors. We sampled songs from seven countries in Europe and one country in North Africa (Figure 1). The Great Tit is an ideal model species for a study of number of syllables per phrase because the song pattern is quite simple with usually 2 or 3 syllables per phrase which are characteristically loud, sharp and somewhat metallic (Cramp & Perrins 1993). It is often easy to count the number of syllables in the field such that a listening observer and not recordings have been used in some earlier studies (Haftorn 1971, Lehtonen 1983). The species is one of the most frequently studied animal species with regard to ecology and behaviour, but also in terms of acoustics (Slabbekoorn 2013). In addition, the Great Tit is a common species with a wide geographical distribution.

In Finland, the number of syllables per phrase in the Great Tit song has appeared to have declined over a few decades, and increased noise was proposed to be the main reason (Lehtonen 1983). We have studied whether the importance of noise also holds true when comparing the number of syllables per phrase among various populations of the species living in areas with different levels of acoustic noise. In addition, we have analysed the song in relation to a number of other characteristics of the environment, in particular vegetation density and geographic location, testing a number of predictions.

First, based on previous findings (Lehtonen 1983), we expected to find fewer syllables per phrase in noisy than calm areas of the Great Tit's breeding range. Second, we predicted a negative relationship between the number of syllables per phrase and vegetation density. Evidence for such a relationship has been reported for Great Tits in a comparative study that included data from several countries (Hunter & Krebs 1979). According to the Acoustic Adaptation Hypothesis (Morton 1975), long-distance bird song will be selected to be transmitted optimally in a specific habitat, for example when the vegetation affects bird sounds by absorption and scattering. However, a relationship between bird song and vegetation density has not been found in every field study (Brumm & Naguib 2009, Ey & Fischer 2012, Bueno-Enciso et al. 2016, Graham et al. 2017). For instance, the songs of the Rufous-collared Sparrow *Zonotrichia capensis* were longer, and with slower trills, in forest habitats compared to open grassland and scrub habitats (Handford & Loughheed 1991). However, another study of 367 species of songbirds found that shorter songs with fewer syllables per song were more common in forest habitats (Crouch & Mason-Gamer 2019). Reverberation might be important as syllables with low frequency modulation like Great Tit might lead to longer and louder signals after transmission in forests (Slabbekoorn et al. 2002).

Last, we studied the number of syllables per phrase in Great Tit songs in relation to latitude, longitude and altitude across Europe. Bird signals can vary geographically (Marler & Tamura 1964, Irwin et al. 2001, Singh & Price 2015), which has been found in the Great Tit (Hunter & Krebs 1979, Bergman 1980, Lehtonen 1983). For instance, bird song complexity may increase at higher latitudes (Weir & Wheatcroft 2011, Kaluthota et al. 2016). However, current evidence does not seem sufficient to consider this pattern a general rule (Najar & Benedict 2019). Although there is a growing interest in latitudinal effects on animal life history and behaviour, including bird song (Kaluthota et al. 2016), it has been difficult to develop reasonable predictions. A challenge has been to take into account the concomitant influence of the ecological context, including the role of acoustic divergence (Wilkins et al. 2013). More attention should also be given to the characteristics of the focal species and their local populations, such as territoriality, breeding density and sex ratio. Not only environmental noise, but also the social context may affect reception of signals in Great Tits (Snijders et al. 2017). The two functions of male song, defence of territory and mate attraction, may not always have similar importance, and the physical distance to the respective receivers may vary with the local densities of males and females.

Below we have assumed that the population density of the Great Tit decreases in general with increasing latitude (Sasvari & Orell 1992), and that variation in density may affect the two primary functions of male song, namely territory defence and mate attraction. The

Table 2. Change in the characteristics of male Great Tit songs in relation to environmental variation. + = increase, - = decrease, 0 = no change.

Variable		References
Season		
Song length including pauses before and after egg-laying compared with egg-laying period	-	Mace 1987
Number of syllables per phrase relative to egg-laying date	0	Bueno-Enciso et al. 2016
Song frequency during female fertility period	-	Halfwerk et al. 2011a
Time of day		
Urban birds start singing earlier in the morning than rural birds	+	Bergen & Abs 1997, Bermúdez-Cuamatzin et al. 2020
Geography		
Frequencies and longitude	0	Slabbekoorn & den Boer-Visser 2006)
Frequencies and latitude	0	Slabbekoorn & den Boer-Visser 2006
Proportion of three syllables per phrase and latitude	-	Bergman 1980
Maximum frequency, frequency range, and number of syllables per phrase with latitude, longitude and altitude	0	Hunter & Krebs 1979
Vegetation, habitat		
Maximum frequency in forests compared with woodlands	-	Hunter & Krebs 1979
Minimum frequency in forests compared with woodlands	0	Hunter & Krebs 1979
Frequency range in forests compared with woodlands	0	Hunter & Krebs 1979
Number of syllables per phrase in forests compared with woodlands	-	Hunter & Krebs 1979
Number of syllables per phrase and greater tree/bush density	0	Bueno-Enciso et al. 2016
	-	Hunter & Krebs 1979
Density (higher density or smaller territory size)		
Number of syllables per phrase	0	Lehtonen 1983, Bueno-Enciso et al. 2016
	+	Hunter & Krebs 1979
Maximum frequency	+	Hunter & Krebs 1979
Minimum frequency	+	Hamao et al. 2011
Frequency range	+	Hunter & Krebs 1979
Song duration (number of phrases per song)	+	Hamao et al. 2011
Male quality		
Number of syllables per phrase (male age, tarsus length, condition)	0	Bueno-Enciso et al. 2016
Repertoire size, strophe length, maximum and minimum frequency (larger black ties)	+	Ferrer et al. 2012
Sex ratio, skewed to fewer females		
Number of song periods and length of song periods	+	Krebs et al. 1981
Frequency of song types	0	Krebs et al. 1981

first function of the song for territorial defence could be more important in the south whereas the second function for mate attraction may be more relevant in the north. In high density areas at southern latitudes, it may be of prime importance to defend a breeding territory from male neighbours and floaters, thus selecting for complex songs with large song repertoires or more intense singing to match counter singing with male rivals in the immediate surroundings (McGregor et al. 1992, Dabelsteen et al. 1996). In low density areas at north sites, Great Tits often leave their territory in winter (Haftorn 1971, Cramp & Perrins 1993, Bye 2006). Mated pairs may also split up because of male

social dominance at feeding sites (Hansen & Slagsvold 2004). Thus, there may sometimes be a lack of females. In Norway, a female removal study showed that when a male Great Tit lost his mate early in the breeding season, he had great difficulty with remating, although the female was removed early in the breeding season (Slagsvold et al. 1994). In this species, females may primarily base their mate choice on the quality of the territory, including suitable nest and roosting sites, and less on the quality of the male song (Krebs 1977, Krebs et al. 1978). Thus, in the north, we suggest that it may be relatively more important to be detected at all by other males and by prospecting females, and thus

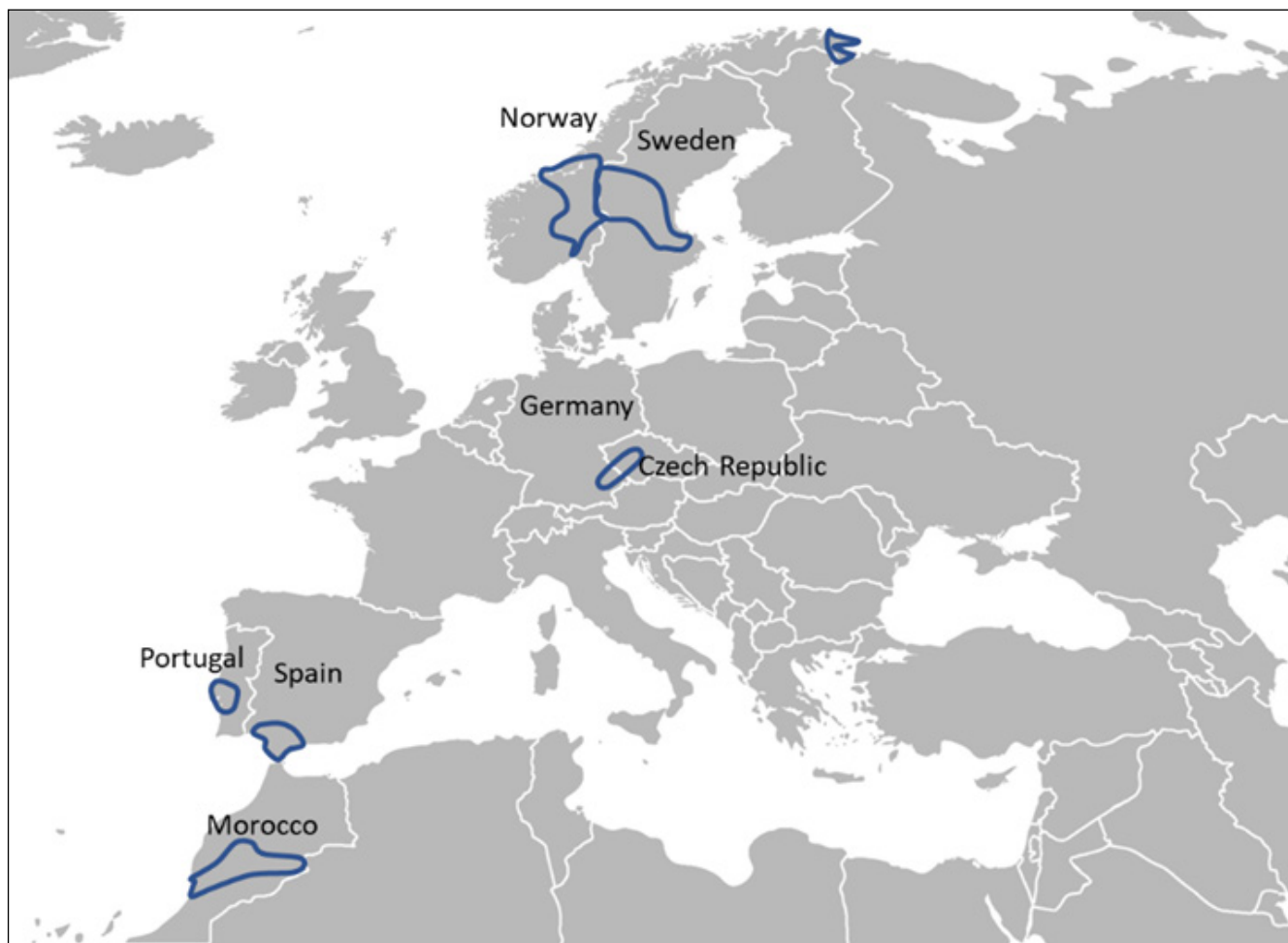


Figure 1. Map showing the investigated areas in Europe and Morocco. In Morocco, Great Tits were only observed in the western part of the country. Map source: Wikimedia Commons (<https://commons.wikimedia.org/wiki/File:BlankMap-Europe-v4.png>).

signal presence with a simple, long-reaching song. We therefore predicted that in the Great Tit, the number of syllables per phrase would be negatively correlated with increasing latitude. Similarly, a negative relationship with number of syllables may also exist with increasing altitude. However, the predicted pattern would depend on how breeding density and the sex ratio change with altitude, whether males and females split in winter, and to which extent individuals move temporarily up and down the altitudinal gradient. Great Tits prefer to breed in relatively dense woodlands and deciduous forests and forest patches, but also in gardens and parks, and thus we included local vegetation density in the analyses. A number of environmental factors may influence male Great Tit songs, and we provide an overview of the relationships reported in the literature (Table 2).

METHODS

Study area and methods

In 2016–19, a total of 762 songs of Great Tits were recorded in the field by visiting 590 different sampling points with singing Great Tits in eight countries (Figure 1, Table 3). All information about the song, and the

characteristics of the local habitat and the vegetation, were written down immediately when birds were observed in the field. There was no random selection of areas to visit but mostly several different areas were visited in each country, and all songs heard well were included.

The songs were noted by listening and without recording with specialized bio-acoustic equipment. Recording is necessary when investigating the songs of most bird species, but here the human ear of an experienced observer was a good instrument to categorize the clear and simple song of the Great Tit. The same method has also been used by previous researchers. In the present study, the focal singing male was always approached so that the details in the song were well categorized. In noisy areas, the number of syllables was only noted at short distances when the singing was clearly heard, and no registrations close to airports were made during take-off or landing of planes. Also, no registrations were included in a few cases when we were unsure about the number of syllables. Thus, we think the data from different sites are comparable, also because they were collected by a single person (MH). In addition, we compared observations both by listening to and by inspecting sonograms for Great Tit

Table 3. The number of field observations of singing male Great Tits according to the number of syllables per phrase and the country of investigation.

Country	Syllables per phrase				Total
	1	2	3	4	
Morocco	0	6	3	2	11
Spain	10	65	46	10	131
Portugal	2	25	4	0	31
Germany	0	3	0	0	3
Czech Republic	0	1	0	0	1
Sweden	1	54	11	1	67
Finland	1	6	0	0	7
Norway	36	395	80	0	511
Total	50	555	144	13	762

songs available at the Xeno-canto repository for sound recordings (<https://Xeno-canto.org/>). Songs of Great Tits were recorded by citizen science observers in the same areas that we visited, namely in southern Spain (Andalucía), the central region of Portugal and across large areas of Norway (Figure 1). The songs on Xeno-canto from Morocco were too few for comparison, and many of the songs from Finland and Sweden had an unusual structure based on the descriptions given by the original observers. In each of the study areas that we also visited in the field, all Xeno-canto recordings were analysed and included if the song characteristics were determined.

For each male Great Tit heard singing, we noted down the number of syllables per phrase. Each male was observed until it was well heard and information about different variables had been recorded, thus lasting from about two minutes to more than 15 minutes per male.

For Great Tits, it is easy to distinguish and categorize the syllables in the song phrases. The phrases contain only one or a few syllables (1–4 in our study), for example ti-ti-tu; ti-ti-tu; ti-ti-tu describing three phrases with three syllables each, or ti-tu; ti-tu; ti-tu; ti-tu describing four phrases with two syllables each. Normally it is easy to categorize the song, however, some males may have different numbers of syllables in different phrases, and even vary the number of syllables within phrases in the same song, termed a mixed song (Lehtonen 1983). Thus, Great Tits can be variable singers with several song types that follow after each other (Hartshorne 1973, Kroodsma 1982). We avoided all such cases as we included only the first song variant heard from each sampling point each day in our investigation.

A few males performed a so-called intermediate song, meaning that one of the syllables was weak or short and difficult to hear. In such cases, it can be difficult to decide the number of syllables, and whether a phrase contains two or three syllables (Lehtonen 1983). The last syllable may be short or incomplete, and may be described like ti-ti-t (Lehtonen 1983). In such rare cases ($n = 4$), we used the highest number (= three

syllables in this example) when it was possible to hear the number of syllables. If any doubt about the number of syllables, meaning that it was difficult to be certain about the number, the case was excluded.

The reliability of the registrations was tested by playing 26 Great tit songs from Xeno-canto to three persons in addition to the observer (MH) who collected all the data used in the present study. Half of the playback tests were conducted in a noisy environment with music and talk from a radio and the other half in a silent surrounding, and observations from the four persons were compared with the number of syllables per phrase shown in the sonograms.

Variables

In the statistical analyses, the dependent variable was the number of syllables per phrase of the focal singing Great Tit male. Explanatory variables are listed in Table 4. Noise levels were initially classified in four categories according to the level of ambient human created noise: 1 = near silent (≤ 35 dB), 2 = little noise (35–55 dB), 3 = much noise (55–75 dB), and 4 = very noisy (close to airports and busy highways; > 75 dB). For training of the observer, the noise was categorized and thereafter compared with a noise meter (ET-933) 135 times in nice weather at different levels of anthropogenic noise from car traffic. We preferred to use categorization by listening because it was easier to avoid sounds that we did not intend to include in our study, such as variation caused by wind, rain, waves, calls and songs from insects, birds and mammals, and caused by the size and speed of the closest car. To be fully reliable, a noise meter should have been applied to record the noise in the surroundings of each singing Great Tit continuously for a longer period to find the mean noise value, because the urban noise will vary during the day and between workdays and weekends (Halfwerk et al. 2011b, Gill et al. 2015; 2017). To compensate for a lack of noise measurements, we analysed the effects of noise on the target variable by only including the extreme categories 1 and 4, recoded as described in Table 4,

Table 4. Explanatory variables included at the beginning of the GLMM analyses.

Variable	Type of data	Comments
Year	Nominal	
Calendar date	Continuous	1 = 1st January
Time of day	Continuous	To the nearest half an hour
Latitude	Continuous	
Longitude	Continuous	
Altitude	Nominal	1 = ≤ 300m 2 = > 300m
Noise	Nominal	1 = ≤ 35dB, or alternatively 1 = ≤ 75dB 2 = > 75dB
Habitat	Nominal	1 = Deciduous woodland 2 = Mixed woodland 3 = Coniferous woodland 4 = Gardens and parks
Vegetation	Nominal	1 = Dense forest/woodland 2 = Open woodland 3 = Parks and gardens 4 = Bushland

although this selection reduced our sample size from 762 to 303 cases. We also used the full dataset in a second analysis by comparing the results from categories 1–3 combined with those for category 4 (Table 4), thus having possible categorization mistakes only for the sound levels around 75 dB. In addition, we analysed the data without noise as an explanatory variable. Nearly all observations in the field were conducted during weather conditions without strong wind or rain to hear the number of syllables per phrase well, and nearly all anthropogenic noise was caused by car traffic only plus three observations close to both roads and an airport.

Habitat and vegetation were classified within a circle with a radius of about 30 m from the singing male, following a previous method (Rønning 1972). All four habitat types were sometimes described as vegetation category 4 (Bushland; Table 4) if they contained small trees and bushes and not tall trees. Time of day was recorded as the closest half an hour, but 305 cases did not have this information. An alternative was to use time relative to sunrise, but several observations were made north of the Polar Circle where the sun was always above the horizon during our fieldwork. Latitude and longitude were determined using Google maps and recorded as continuous variables to the nearest 0.5 degrees. A more detailed positioning was unnecessary because of the great geographical span of

the visited sites.

Sampling point number was included as random factor. Only the first song type heard from the same sampling point was recorded each day. If the number of syllables per phrase was noted again on the same sampling point another day, the same sampling point number was used as for the earlier observations in the same year. The sampling point number was changed every year even if the singing came from the same sampling point as visited in an earlier year. Unfortunately, we did not gather data on territory density (Ripmeester et al. 2010), the number of males at different nesting stages (Stuart et al. 2019), or whether or not other males were singing in the vicinity of the focal males (Deoniziak & Osiejuk 2021).

In the field, several males were sometimes heard singing at the same time from different sampling points, and then all birds were sampled. Neighbouring male Great Tits often share song types (McGregor & Krebs 1982, Slabbekoorn & den Boer-Visser 2006, Rivera-Gutierrez et al. 2010). However, Great Tits learn their song from several males throughout life (McGregor et al. 1981, McGregor & Krebs 1982, McGregor & Krebs 1989, Franco & Slabbekoorn 2009), and adjust some parts of the vocalizations to enhance transmission in each respective territory (Bueno-Enciso et al. 2016). On the other hand, a second study found that song

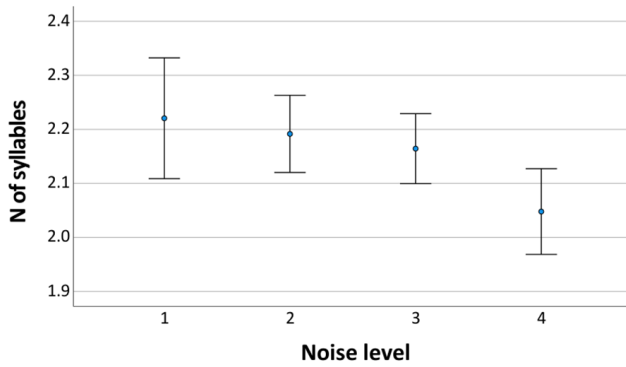


Figure 2. The number of syllables per phrase (± 2 SE) for Great Tit songs in areas with various levels of anthropogenic noise, from near silent (level 1 ≤ 35 dB, $n = 136$), little noise (level 2 35–55 dB, $n = 240$), much noise (level 3 55–75 dB, $n = 219$) to very noisy (level 4 > 75 dB, $n = 167$). In the GLMM analyses, we compared noise level 1 versus level 4, or a combination of levels 1-3 versus level 4 (see text for more information).

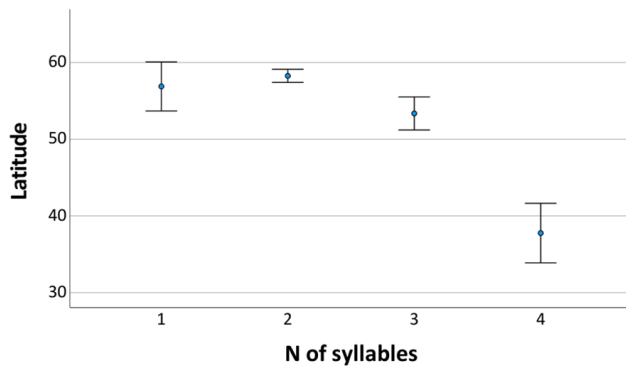


Figure 3. Mean latitude (± 2 SE) of the sampling points where the different number of syllables per phrase were observed (the number of sampling points with the various numbers of syllables per phrase were 50, 555, 144 and 13 respectively).

repertoire size and composition were highly repeatable both between years and after confrontation with a novel song (Rivera-Gutierrez et al. 2011). Due to the variance in the results reported, we opted to treat observations from each sampling point as independent between years but with sampling point number as a random factor within years.

Generalized linear mixed models (GLMM) were used (IBM 2021) because they reduce variability in responses that are associated with random factors rather than the conditions of experimental interest, thus reducing Type I error rate (Lo & Andrews 2015). GLMM may be the best tool for analyzing non-normal data that involve random effects (Bolker et al. 2009). Spearman rank correlation was used to relate the explanatory variables against each other, and Mann-Whitney U-test to compare our observations of songs with Xeno-canto recordings. Statistical tests were two-tailed with an alpha level of 0.05. We are aware of an ongoing discussion about the relative merits of null hypothesis and statistical testing (NHST) versus

IT-based inference (Mundry 2011), but our data were well suited for analyses based on NHST methods (Burnham & Anderson 2002).

In the GLMM analyses, we used multinomial probability distribution of the dependent variable and cumulative logit link function. Using graphical tools (Zuur et al. 2010), the histogram with Regression Standardized Residuals and Frequency showed normal distribution (Lo & Andrews 2015). The data in the models seemed to have a constant error variance (homoscedasticity) and no overdispersion (Burnham & Anderson 2002). From the global model (Burnham & Anderson 2002), we selected various candidate models with the explanatory variables included by using backwards stepwise removal of explanatory variables and Akaike's Information Criterion (AIC).

The data exploration (Burnham & Anderson 2002, Bolker et al. 2009, Zuur et al. 2010) showed outliers for date of observation and latitude. Outliers were caused by early and late observations in January or December, and by observations in the far south of Morocco and southern Spain or sites in northern Norway. The outliers were not removed when applying the \log_{10} transformation and so no such transformation was used. However, the data were not skewed by the outliers, and GLMM may still yield efficient estimators although the data may be unbalanced (SPSS 2005). The random effects were not significant (p -values about 0.5).

RESULTS

The reliability test about the number of syllables per phrase in controlled playbacks of the Great Tit song, showed accordance with the sonograms for three of four observers. The fourth person was not responsible for the registrations in the present study and mistakenly recorded three syllables per phrase, instead of the correct two syllables, for two weak and fast singing Great Tits in noisy surroundings. By moving closer to the sound source to investigate the uncertainty, as was done in the field, the mistakes were corrected.

The analysis of the number of syllables per phrase with all explanatory variables included, gave no significant effect of time of day ($F_{1,168} = 0.584$, $p = 0.756$). Time of day was excluded in the further analyses because missing information for this variable reduced our sample size.

All Spearman rank correlation values between the explanatory variables were below the suggested limit of 0.7 (Dormann et al. 2013). The Variance Inflation Factors (VIF) were between 1.0 and 1.9, which are within the range for recommended values (Burnham & Anderson 2002, Zuur et al. 2010).

The best model with noise either ≤ 35 dB or > 75 dB as the dependent variable only included two variables, namely noise and latitude. The first variable removed

Table 5. GLMM analysis of number of syllables per phrase of Great Tit songs as the dependent variable, and the background noise and the latitude of the focal male's territory as the explanatory variables ($n = 762$). The target variable was ordinal, resulting in a multinomial model, and the traditional intercept term was replaced with a set of threshold parameters that relate to the cumulative probability of the dependent categories. Noise 1 is noise category 1 compared with the highest category 2. The two columns to the right show the 95% CI for the coefficients. The significant explanatory variables are in bold.

Model term	Coefficient	SE	t	p	CI Lower	CI Upper
Threshold 1	-2.572	0.9586	-2.684	0.008	-4.459	-0.686
Threshold 2	1.394	0.9485	1.470	0.143	-0.472	3.261
Threshold 3	3.824	1.0082	3.793	< 0.001	1.840	5.808
Noise 1	0.513	0.2601	1.973	0.049	0.001	1.025
Latitude	-0.020	0.0135	-1.473	0.142	-0.046	0.007

was day, followed by altitude, habitat, year and vegetation. Vegetation may give a better description of vegetation density than habitat, and vegetation density is known to influence some bird song properties (Hunter & Krebs 1979, Bueno-Enciso et al. 2016, Graham et al. 2017, Hill et al. 2017). However, $\Delta AIC_C > 2$ ($\Delta AIC_C = 24$) between the models including only noise and latitude versus a model that included vegetation in addition. Vegetation was therefore not included in the further analysis (Burnham & Anderson 2002). Therefore, the final model ended with noise and latitude as the only explanatory variables (Table 5). The result from the GLMM analysis was only nearly significant with latitude and noise as explanatory variables (corrected model, $F_{2,298} = 2.803$, $p = 0.062$). The number of syllables was higher in areas with little noise (≤ 35 dB) versus high anthropogenic noise (> 75 dB). It was only a weak and not significant tendency that the number of syllables per phrase decreased with increasing latitude (Table 3, Table 5).

To use more of our collected data, noise levels 1–3 were combined to a new noise level (≤ 75 dB), while former level 4 was redefined to another level (> 75 dB). The model selection procedure gave these two noise levels, combined with latitude, as the only explanatory variables kept in the best model. The GLMM analysis resulted in a significant model ($F_{2,757} = 15.204$, $p < 0.001$). Both noise (Coefficient = 0.542, SE = 0.194, $t = 2.798$, $p = 0.005$) and latitude (Coefficient = -0.034, SE = 0.007, $t = -4.962$, $p < 0.001$) were significant, meaning that the number of syllables per phrase decreased with both higher noise levels and northwards. The relationship between the number of syllables per phrase and noise is shown in Figure 2, and the relationship with latitude is shown in Figure 3.

The same model selection procedure without noise as an explanatory variable, resulted in latitude and altitude as explanatory variables in the best model. The GLMM analysis resulted in a significant corrected model ($F_{2,757} = 12.195$, $p < 0.001$). However, only latitude (Coefficient = -0.032, SE = 0.007, $t = -4.661$, $p < 0.001$) significantly explained the variation in number of syllables per phrase, and not altitude (the lowest

altitude category compared with the highest category: Coefficient = -0.347, SE = 0.264, $t = -1.315$, $p = 0.189$). Thus, the number of syllables per phrase decreased northwards but did not change significantly with other explanatory variables.

The sonograms for Great Tits available at Xeno-canto had a similar number of syllables per phrase as found for our field observations in Norway (2.13 and 2.09, $n = 63$ and 523, respectively; Mann-Whitney U-test, $z = -0.580$, $p = 0.562$) and in Spain (2.35 and 2.43, $n = 57$ and 131; $z = -0.60$, $p = 0.550$), but they were significantly higher than our values for Portugal (2.45 and 2.06, $n = 20$ and 31, $z = -2.34$, $p = 0.019$). Based on only the recordings from Xeno-canto, the number of syllables per phrase for Norway was nearly significantly lower than in Spain ($n_1 = 63$, $n_2 = 57$, $z = -1.83$, $p = 0.067$) and significantly lower than in Portugal ($n_1 = 63$, $n_2 = 20$, $z = -2.28$, $p = 0.023$), thus supporting our GLMM results that the number of syllables per phrase is lower at higher latitudes.

DISCUSSION

The main results were that the number of syllables per phrase in the Great Tit decreased with high levels of anthropogenic noise, and decreased with increasing latitude, supporting our predictions. When these two variables were taken into account, there was no significant effect of year of study, type of habitat and vegetation, calendar date, time of day, longitude or altitude on the song structure of Great Tits.

The number of syllables per phrase varied between one and four, a number and variation that seemed easy to assess in the field. The singing males were approached in the field, ensuring that the number of syllables was as correctly observed as possible. We may have lost or misinterpreted some syllables when the number of syllables per phrase was high. However, we do not think scoring complex songs was a problem because the phrases were repeated many times during the observations of a focal male and the human observer was usually located quite close to the singing birds.

Comparing our observations of syllables from listening with the sonograms for 140 Xeno-canto recordings of singing Great Tits from the same areas, we categorized the number of syllables per phrase incorrectly only twice compared with the sonogram information. The two mistakes may have been caused by reverberation that made it difficult to count the correct number of syllables per phrase in the sonograms. Moreover, our reliability test indicated that the counting of the number of syllables per phrase was valid.

We used the human ear to categorize the noise level, and only used a noise meter for training of the categorizations. The noise meter training was conducted mostly in nice weather and in presence of more or less car traffic. However, there might be some mistakes in the classifications when the noise level experienced was close to the value distinguishing two categories. When we first categorized the sound level into one of our four categories and thereafter used the noise meter to compare, a majority of categorizations were correct (96%, 129 of 135). The six incorrect cases were all in the nearest category (five categorized too low and one too high). Nevertheless, we reduced the number of noise categories from four to two in the analysis to avoid any mistakes, and in two categories with possible mistakes only occurring around 75 dB. Our results are credible and that there is no reason that potential mistakes should vary geographically. For both the alternatives with modified noise categories, noise significantly affected the number of syllables per phrase.

The noise categorization was made at the same time as the number of syllables per phrase was counted, but noise-levels may change a lot during the day (Gill et al. 2017). It might therefore be better to measure the mean noise-level during a certain period, for instance during a week just prior to egg laying, to determine the mean level of exposure for each focal territory. However, it might still be difficult to separate between anthropogenic and natural sources of noise.

Anthropogenic noise

Anthropogenic noise is widespread and a main source is noise from vehicle traffic on public roads, as also experienced in our study. Road systems can affect large areas in some countries, including 15–20% of the land area in the United States (Forman & Alexander 1998, Forman 2000). Communication through masking noise may be difficult for wild animals. For instance, transmission efficiency is significantly lower in cities compared to rural areas (Mockford et al. 2011). Noise has also been found to reduce signal detection in Great Tits (Pohl et al. 2009) as well as the degree of female responses (Halfwerk et al. 2012).

In noisy environments, the two modifications of the song most often reported in the literature have been alterations of the frequency and shifts in the amplitude

(Katti & Warren 2004), while a change in song complexity has been considered to be less common (Ey & Fischer 2012). In North American passerines, a common effect of noise seems to be a reduction in frequency bandwidths rather than a change in the diversity of the syllables (Cardoso et al. 2020). In the Helsinki region in Finland, the number of syllables per phrase of Great Tit songs declined between 1947 and 1981 without any changes in territory size (Lehtonen 1983). The author therefore concluded that the result was caused by an increase in anthropogenic noise. In the present study, we did not find any effect of year, but our study was also conducted over a short 4-year time period.

In areas with urban noise, Great Tits may change song frequencies and also have shorter songs (Slabbekoorn & Peet 2003, Slabbekoorn & den Boer-Visser 2006, Halfwerk & Slabbekoorn 2009). Males may also use certain positions in the territory to optimise sound transmission (Hunter 1980). The present study shows that the reduction in the number of syllables per phrase may be another adaptation to noisy habitats, although in a previous study of Great Tits, no such relationship was found (Hunter & Krebs 1979). However, apparently, in the latter study, areas with loud anthropogenic noise were not sampled. In the present study, effects only occurred at very noisy sites (level 4, Figure 2). Slabbekoorn and den Boer-Visser (2006) found that the first syllable was significantly shorter in cities compared with neighbouring rural areas, but a pattern of fewer syllables per phrase in noisy areas was not confirmed. However, the noise level was not measured (Slabbekoorn & den Boer-Visser 2006). In our study, we found the highest noise category along busy roads outside the cities and not in the cities where vehicle speed was lower. The song of the Great Tit is simpler than that of many other songbirds. The message may therefore reach the receivers even through quite high levels of noise, except in very noisy environments, where the strength of the noise may reach above the sounds from most singing birds. Presumably, the type of song of the focal species studied is important.

Noisy habitats are unlikely to be preferred by Great Tits, and may thus be settled by males of low quality that may sing differently from other males (Slabbekoorn & den Boer-Visser 2006). Females may prefer males with larger than smaller song repertoires. However, song repertoire does not seem to be significant factor in the Great Tit (McGregor & Krebs 1982, Baker et al. 1986, Tietze 2018), nor in songbirds in general (Byers & Kroodsma 2009). Thus, the problem of transmitting the signal through a very noisy environments may be of greater importance than having a large song repertoire. Reducing the number of syllables per phrase in a noisy surrounding might therefore have a selective advantage given that such males are not judged by the females to be of poor quality.

Social environment and latitude

Birds may modify their songs in relation to features of their social environment, including the number of males which can compete by song matching, to the difficulty of obtaining a mate, or the distance to the respective receivers of the signal (Grabarczyk et al. 2020, Deoniziak & Osiejuk 2021). Few studies have taken these alternate factors into account.

In a study of Great Tits in different habitats and ten countries, the number of syllables per phrase was negatively correlated with territory size (Hunter & Krebs 1979). The finding was consistent with our prediction that males will have fewer syllables per phrase in areas with a low density of males such as our field sites at high latitudes. In contrast, the distances to the neighbours may be short in southern areas, even for males with relatively large territories.

Unfortunately, our study did not include the population density or territory size of the focal Great Tits, nor the local sex ratio. However, our study of song in relation to latitude may have some relevance. We found a significant reduction of the number of syllables with increasing latitude, both when using our field observations and in a separate analysis of recordings from Xeno-canto. The findings supported our prediction that was based on two assumptions, namely that breeding density of the Great Tit decreases with increasing latitude (Sasvari & Orell 1992), making song matching with many close male neighbours to defend the territory less important, and the assumption that there may be a shortage of females at high latitudes, selecting for a simple, long-reaching signal that can readily be detected and located by prospecting females. At high latitudes, birds may even benefit from having close neighbours due to early warnings from other birds of approaching predators (Moks et al. 2016, Tolvanen et al. 2018).

Evidently, the relationship between bird song and latitude needs more attention. An earlier study of Great Tits included some of the same countries as ours, but no relationship was found between the number of syllables per phrase and latitude (Hunter & Krebs 1979). Studies of several hundred species, have found an increase in the number of syllables per song, song length, song complexity and/or spectral entropy, with increasing distance from the Equator, both within and among some of the study species (Weir & Wheatcroft 2011, Kaluthota et al. 2016, Crouch & Mason-Gamer 2019). However, latitudinal trends may not necessarily apply in general to songbirds (Najar & Benedict 2019), and especially not for species with a rather simple song such as the Great Tit (Weir & Wheatcroft 2011). In fact, some comparative studies of fringillids (Fringillidae) and leaf warblers (Phylloscopidae) have shown reductions in song complexity with increasing latitude (Handley & Nelson 2005, Tietze et al. 2015).

In the present study, no explanatory variables

seemed to have an impact on the number of syllables per phrase in the Great Tit song except for background levels of environmental noise and latitude. In a study of Great Tits in Spain, the number of syllables per phrase was not affected by any of the explanatory variables that were investigated, including date relative to egg laying, breeding density, tree diameter, tree cover, shrub cover, ground cover, male age, tarsus length and male condition (Bueno-Enciso et al. 2016). Likewise, in a study of Great Tit songs across Europe and Morocco, no significant relationship was found between the number of syllables per phrase and longitude (Hunter & Krebs 1979). In a review of the song of various animal species, there was no general influence of habitat type on temporal features or repetition rate (Ey & Fischer 2012). However, in their study of Great Tits, Hunter & Krebs (1979) found that the number of syllables per phrase was significantly lower in areas with a high rather than a low density of trees. The latter finding is consistent with our prediction with regard to vegetation density, although the prediction was not supported in our study.

Xeno-canto recordings

We conclude that our results were due to variation in the songs of the Great Tit and were not biased by the method used. The song of the Great Tit is quite simple and repetitive, and each male has a small repertoire compared to most other songbirds.

From the Xeno-canto sonograms, it is evident that the recordings have been made in areas with less ambient noise than in the areas we visited that had the highest background noise (> 75 dB). However, analysing the data in Xeno-canto for Spain, three songs seemed to have been recorded in areas with quite strong traffic noise (possibly around 70 dB), with 1, 1 and 2 syllables per phrase, respectively, both according to the sonograms and our listening.

The Xeno-canto recordings may be a biased sample if observers are more likely to record and upload unusual songs than normal and common ones, as we found when evaluating sonograms from Finland and Sweden. Recently, similar biases in reports of bird appearances on the Internet, have been discussed (Husby 2017) and demonstrated (Zbyryt et al. 2021) with regard to plumage colour. Uploaded photos contained a higher percentage of birds with colour aberrations than found in nature.

Conclusion

Bird song is influenced by a range of biotic and abiotic factors (Catchpole & Slater 2008, Crouch & Mason-Gamer 2019). Tests can be refined by studying song variation within species in relation to several environmental variables (Hunter & Krebs 1979, Irwin 2000, Collins et al. 2009). We sampled one characteristic of the Great Tit song, the number of

syllables per phrase, across eight countries and found that the most important explanatory variables were anthropogenic noise and the latitude of the focal site. We recommend more investigations at the species level that pay attention to these variables but that also take into account the focal social environment, and thus keep in mind the primary functions of male song, namely to defend a territory and to attract a mate.

REFERENCES

- Akçay C, Porsuk YK, Avsar A, Cabuk D & Bilgin CC. 2020. Song overlapping, noise, and territorial aggression in Great Tits. *Behavioral Ecology* **31**: 807–814.
- Baker MC, Bjerke TK, Lampe H & Espmark Y. 1986. Sexual response of female Great Tits to variation in size of males' song repertoires. *American Naturalist* **128**: 491–498.
- Bergen F & Abs M. 1997. Etho-ecological study of the singing activity of the Blue Tit (*Parus caeruleus*), Great Tit (*Parus major*) and Chaffinch (*Fringilla coelebs*). *Journal für Ornithologie* **138**: 451–467.
- Berger-Tal O, Wong BBM, Candolin U & Barber J. 2019. What evidence exists on the effects of anthropogenic noise on acoustic communication in animals? A systematic map protocol. *Environmental Evidence* **8** (Suppl 1): art18.
- Bergman, G. 1980. Die Veränderung der Gesangmelodie der Kohlmeise *Parus major* in Finnland und Schweden (The change of song pattern of the Great Tit *Parus major* in Finland and Sweden). *Ornis Fennica* **57**: 97–111.
- Bermúdez-Cuamatzin E, Delamore Z, Verbeek L, Kremer C & Slabbekoorn H. 2020. Variation in diurnal patterns of singing activity between urban and rural Great Tits. *Frontiers in Ecology and Evolution* **8**: art246.
- Bermúdez-Cuamatzin E, Rios-Chelen AA, Gil D & Garcia CM. 2009. Strategies of song adaptation to urban noise in the House Finch: syllable pitch plasticity or differential syllable use? *Behaviour* **146**: 1269–1286.
- Blumenrath SH & Dabelsteen T. 2004. Degradation of Great Tit (*Parus major*) song before and after foliation: Implications for vocal communication in a deciduous forest. *Behaviour* **141**: 935–958.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH & White JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* **24**: 127–135.
- Brumm H & Naguib M. 2009. Environmental acoustics and the evolution of bird song. Pp. 1–33 in M Naguib, K Zuberbühler, NS Clayton & VM Janik (Eds.) *Advances in the Study of Behavior*, Vol. 40. Elsevier Academic Press Inc, San Diego.
- Brumm H & Slabbekoorn H. 2005. Acoustic communication in noise. Pp. 151–209 in Slater PJB, Snowdon CT, Brockmann HJ, Roper TJ & Naguib M (Eds.) *Advances in the Study of Behavior*, Vol. 35. Elsevier Academic Press Inc, San Diego.
- Brumm H & Slater PJB. 2006. Ambient noise, motor fatigue, and serial redundancy in Chaffinch song. *Behavioral Ecology and Sociobiology* **60**: 475–481.
- Brumm H & Zollinger SA. 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour* **148**: 1173–1198.
- Bueno-Enciso J, Ferrer ES, Barrientos R & Sanz JJ. 2016. Habitat structure influences the song characteristics within a population of Great Tits *Parus major*. *Bird Study* **63**: 359–368.
- Bueno-Enciso J, Nunez-Escribano D & Sanz JJ. 2015. Cultural transmission and its possible effect on urban acoustic adaptation of the Great Tit *Parus major*. *Animal Biodiversity and Conservation* **38**: 221–231.
- Burnham KP & Anderson DR. 2002. *Model selection and multimodel inference. A practical information-theoretic approach*. Second Edition. Springer, New York.
- Bye FN. 2006. Kjøttmeis *Parus major*. Pp. 356–357 in Svorkmo-Lundberg T, Bakken V, Helberg M, Mork K, Røer JE & Sæbø S (Eds.) *Norsk VinterfuglAtlas. Fuglenes utbredelse, bestandsstørrelse og økologi vinterstid*. Norsk Ornitologisk Forening, Trondheim.
- Byers BE & Kroodsma DE. 2009. Female mate choice and songbird song repertoires. *Animal Behaviour* **77**: 13–22.
- Cardoso GC, Klingbeil BT, La Sorte FA, Lepczyk CA, Fink D & Flather CH. 2020. Exposure to noise pollution across North American passerines supports the noise filter hypothesis. *Global Ecology and Biogeography* **29**: 1430–1434.
- Cartwright LA, Taylor DR, Wilson DR & Chow-Fraser P. 2014. Urban noise affects song structure and daily patterns of song production in Red-winged Blackbirds (*Agelaius phoeniceus*). *Urban Ecosystems* **17**: 561–572.
- Catchpole CK & Slater PJB. 2008. *Bird song: biological themes and variations*. Cambridge University Press, Cambridge.
- Colino-Rabanal VJ, Mendes S, Peris SJ & Pescador M. 2016. Does the song of the wren *Troglodytes troglodytes* change with different environmental sounds? *Acta Ornithologica* **51**: 13–22.
- Collins SA, de Kort SR, Perez-Tris J & Telleria JL. 2009. Migration strategy and divergent sexual selection on bird song. *Proc R Soc B* **276**: 585–590.
- Cramp S & Perrins CM. 1993. *The birds of the Western Palearctic*. Vol. 7: Flycatchers to shrikes. Oxford University Press, Oxford.
- Crouch NMA & Mason-Gamer RJ. 2019. Identifying ecological drivers of interspecific variation in song complexity in songbirds (Passeriformes, Passeri). *Journal of Avian Biology* **50**: 14.
- Dabelsteen T, McGregor PK, Shepherd M, Whittaker X & Pedersen SB. 1996. Is the signal value of overlapping different from that of alternating during matched singing in Great Tits? *Journal of Avian Biology* **27**: 189–194.
- Deoniziak K & Osiejuk TS. 2016. Disentangling relations among repertoire size, song rate, signal redundancy and ambient noise level in European songbird. *Ethology* **122**: 734–744.
- Deoniziak K & Osiejuk TS. 2019. Habitat-related differences in song structure and complexity in a songbird with a large repertoire. *BMC Ecology* **19**: art40.
- Deoniziak K & Osiejuk TS. 2021. Seasonality and social factors, but not noise pollution, influence the song characteristics of two leaf warbler species. *Plos One* **16**: e0257074.

- Dormann CF, Elith J, Bacher S, Buchmann CCG, Carre G, Marquez JRG, Gruber B, Lafourcade B, Leitaó PJ, Munkemüller T, McClean C, Osborne PE, Reineking B, Schroder B, Skidmore AK, Zurell D & Lautenbach S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**: 27–46.
- Dowling JL, Luther DA & Marra PP. 2012. Comparative effects of urban development and anthropogenic noise on bird songs. *Behavioral Ecology* **23**: 201–209.
- Emlen ST. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* **41**: 130–171.
- Ey E & Fischer J. 2012. The 'acoustic adaptation hypothesis' – a review of the evidence from birds, anurans and mammals. *Bioacoustics* **19**: 21–48.
- Fernández-Juricic E, Poston R, De Collibus K, Morgan T, Bastain B, Martin C, Jones K & Treminio R. 2005. Microhabitat selection and singing behavior patterns of male House Finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western U.S. *Urban Habitats* **3**: 49–69.
- Ferrer M, de Lucas M, Janss GFE, Casado E, Munoz AR, Bechard MJ & Calabuig CP. 2012. Weak relationship between risk assessment studies and recorded mortality in wind farms. *Journal of Applied Ecology* **49**: 38–46.
- Foppen R & Reijnen R. 1994. The effects of car traffic on breeding bird populations in woodland. 2. Breeding dispersal of male Willow Warblers (*Phylloscopus trochilus*) in relation to the proximity of a highway. *Journal of Applied Ecology* **31**: 95–101.
- Forman RTT. 2000. Estimate of the area affected ecologically by the road system in the United States. *Conservation Biology* **14**: 31–35.
- Forman RTT & Alexander LE. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**: 207–231.
- Francis CD, Ortega CP & Cruz A. 2009. Noise pollution changes avian communities and species interactions. *Current Biology* **19**: 1415–1419.
- Franco P & Slabbekoorn H. 2009. Repertoire size and composition in Great Tits: a flexibility test using playbacks. *Animal Behaviour* **77**: 261–269.
- Gill SA, Grabarczyk EE, Baker KM, Naghshineh K & Vonnhof MJ. 2017. Decomposing an urban soundscape to reveal patterns and drivers of variation in anthropogenic noise. *Science of the Total Environment* **599**: 1191–1201.
- Gill SA, Job JR, Myers K, Naghshineh K & Vonnhof MJ. 2015. Toward a broader characterization of anthropogenic noise and its effects on wildlife. *Behavioral Ecology* **26**: 328–333.
- Goodwin SE & Podos J. 2013. Shift of song frequencies in response to masking tones. *Animal Behaviour* **85**: 435–440.
- Goodwin SE & Shriver WG. 2011. Effects of traffic noise on occupancy patterns of forest birds. *Conservation Biology* **25**: 406–411.
- Grabarczyk EE, Vonnhof MJ & Gill SA. 2020. Social context and noise affect within and between male song adjustments in a common passerine. *Behavioral Ecology* **31**: 1150–1158.
- Grade AM & Sieving KE. 2016. When the birds go unheard: highway noise disrupts information transfer between bird species. *Biology Letters* **12**: 20160113.
- Graham BA, Sandoval L, Dabelsteen T & Mennill DJ. 2017. A test of the Acoustic Adaptation Hypothesis in three types of tropical forest: degradation of male and female Rufous-and-white Wren songs. *Bioacoustics* **26**: 37–61.
- Haftorn S. 1971. *Norges fugler*. Universitetsforlaget, Oslo, Norway.
- Halfwerk W, Bot S, Buikx J, van der Velde M, Komdeur J, ten Cate C & Slabbekoorn H. 2011a. Low-frequency songs lose their potency in noisy urban conditions. *PNAS* **108**: 14549–14554.
- Halfwerk W, Bot S. & Slabbekoorn H. 2012. Male Great Tit song perch selection in response to noise-dependent female feedback. *Functional Ecology* **26**: 1339–1347.
- Halfwerk W, Holleman LJM, Lessells CM & Slabbekoorn H. 2011b. Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology* **48**: 210–219.
- Halfwerk W & Slabbekoorn H. 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Animal Behaviour* **78**: 1301–1307.
- Hamao S, Watanabe M & Mori Y. 2011. Urban noise and male density affect songs in the Great Tit *Parus major*. *Ethology Ecology & Evolution* **23**: 111–119.
- Handford P & Loughheed SC. 1991. Variation in duration and frequency characters in the song of the Rufous-collared Sparrow, *Zonotrichia capensis*, with respect to habitat, trill dialects and body size. *Condor* **93**: 644–658.
- Handley HG & Nelson DA. 2005. Ecological and phylogenetic effects on song sharing in songbirds. *Ethology* **111**: 221–238.
- Hansen BT & Slagsvold T. 2004. Early learning affects social dominance: interspecifically cross-fostered tits become subdominant. *Behavioral Ecology* **15**: 262–268.
- Hartshorne C. 1973. *Born to sing. An interpretation and world survey of bird song*. Indiana University Press, Bloomington.
- Huffeltdt NP & Dabelsteen T. 2013. Impact of a noise-polluted urban environment on the song frequencies of a cosmopolitan songbird, the Great Tit (*Parus major*), in Denmark. *Ornis Fennica* **90**: 94–102.
- Hunter ML. 1980. Microhabitat selection for singing and other behaviour in Great Tits, *Parus major*: Some visual and acoustical considerations. *Animal Behaviour* **28**: 468–475.
- Hunter ML & Krebs JR. 1979. Geographic variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. *Journal of Animal Ecology* **48**: 759–785.
- Husby M. 2017. Colour aberrations in Eurasian Magpies *Pica pica* in Europe. *Ornithological Science* **16**: 111–119.
- IBM. 2021. *IBM SPSS Statistics 27.0.1.0*. Armonk, NY: IBM Corp.
- Irwin DE. 2000. Song variation in an avian ring species. *Evolution* **54**: 998–1010.
- Irwin DE, Bensch S & Price TD. 2001. Speciation in a ring. *Nature* **409**: 333–337.
- Kaluthota C, Brinkman BE, dos Santos EB & Rendall D. 2016. Transcontinental latitudinal variation in song performance and complexity in House Wrens (*Troglodytes aedon*). *Proc R Soc B* **283**: 20152765.

- Katti M & Warren PS. 2004. Tits, noise and urban bioacoustics. *Trends in Ecology & Evolution* **19**: 109–110.
- Krebs JR. 1977. Song and territory in the Great tit *Parus major*. Pp. 47–62 in: Stonehouse B & Perrins C (Eds.) *Evolutionary Ecology*. Palgrave, London.
- Krebs JR, Ashcroft R & Webber M. 1978. Song repertoires and territory defence in the Great Tit. *Nature* **271**: 539–542.
- Krebs JR, Avery M & Cowie RJ. 1981. Effect of removal of mate on the singing behavior of Great Tits. *Animal Behaviour* **29**: 635–637.
- Kroodsma DE. 1982. Song repertoires: problems in their definition and use. Pp. 125–146 in Kroodsma DE, Miller EH & Ouellet H (Eds.) *Acoustic communication in birds*. Volume 2. Song learning and its consequences. Academic Press, New York.
- Kunc HP & Schmidt R. 2021. Species sensitivities to a global pollutant: A meta-analysis on acoustic signals in response to anthropogenic noise. *Global Change Biology* **27**: 675–688.
- Lampe HM, Larsen ON, Pedersen SB & Dabelsteen T. 2007. Song degradation in the hole-nesting Pied Flycatcher *Ficedula hypoleuca*: Implications for polyterritorial behaviour in contrasting habitat-types. *Behaviour* **144**: 1161–1178.
- Lehtonen L. 1983. The changing song patterns of the Great Tit *Parus major*. *Ornis Fennica* **60**: 16–21.
- Lo S & Andrews S. 2015. To transform or not to transform: using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology* **6**: 1–16.
- Lombard E. 1911. Le signe de l'élévation de la voix. *Ann. Malad. l'Oreille Larynx* **37**: 101–119.
- Mace R. 1987. Why do birds sing at dawn? *Ardea* **75**: 123–132.
- Marler P & Tamura M. 1964. Culturally transmitted patterns of vocal behavior in sparrows. *Science* **146**: 1483–1486.
- McGregor PK, Dabelsteen T, Shepherd M & Pedersen SB. 1992. The signal value of matched singing in great tits: evidence from interactive playback experiments. *Animal Behaviour* **43**: 987–998.
- McGregor PK & Krebs JR. 1982. Song types in a population of Great Tits (*Parus major*): their distribution, abundance and acquisition by individuals. *Behaviour* **79**: 126–152.
- McGregor PK & Krebs JR. 1989. Song learning in adult Great Tits (*Parus major*): effects of neighbours. *Behaviour* **108**: 139–159.
- McGregor PK, Krebs JR & Perrins CM. 1981. Song repertoires and lifetime reproductive success in the Great Tit (*Parus major*). *American Naturalist* **118**: 149–159.
- Mendes S, Colino-Rabanal VJ & Peris SJ. 2017. Acoustic adaptation in *Turdus leucomelas* (Passeriformes: Turdidae) songs to different levels of anthropogenic noise, in the metropolitan area of Belem, Para, Brazil. *Revista De Biologia Tropical* **65**: 633–642.
- Mockford EJ & Marshall RC. 2009. Effects of urban noise on song and response behaviour in great tits. *Proc R Soc B* **276**: 2979–2985.
- Mockford EJ, Marshall RC & Dabelsteen T. 2011. Degradation of rural and urban Great Tit song: testing transmission efficiency. *Plos One* **6**: e28242.
- Moks K, Tilgar V, Thomson RL, Calhim S, Järvisto E, Schuett W, Velmala W & Laaksonen T. 2016. Predator encounters have spatially extensive impacts on parental behaviour in a breeding bird community. *Proc R Soc B* **283**: 20160020.
- Morton ES. 1975. Ecological sources of selection on avian sounds. *American Naturalist* **109**: 17–34.
- Mundry R. 2011. Issues in information theory-based statistical inference—a commentary from a frequentist's perspective. *Behavioral Ecology and Sociobiology* **65**: 57–68.
- Najar N & Benedict L. 2019. The relationship between latitude, migration and the evolution of bird song complexity. *Ibis* **161**: 1–12.
- Pohl NU, Leadbeater E, Slabbekoorn H, Klump GM & Langemann U. 2012. Great Tits in urban noise benefit from high frequencies in song detection and discrimination. *Animal Behaviour* **83**: 711–721.
- Pohl NU, Slabbekoorn H, Klump GM & Langemann U. 2009. Effects of signal features and environmental noise on signal detection in the Great Tit, *Parus major*. *Animal Behaviour* **78**: 1293–1300.
- Reijnen R & Foppen R. 1991. Effect of road traffic on the breeding site tenacity of male Willow Warblers (*Phylloscopus trochilus*). *Journal für Ornithologie* **132**: 291–295.
- Reijnen R & Foppen R. 1994. The effects of car traffic on breeding bird populations in woodland. 1. Evidence of reduced habitat quality for Willow Warblers (*Phylloscopus trochilus*) breeding close to a highway. *Journal of Applied Ecology* **31**: 85–94.
- Reijnen R & Foppen R. 1995. The effects of car traffic on breeding bird populations in woodland .4. Influence of population-size on the reduction of density close to a highway. *Journal of Applied Ecology* **32**: 481–491.
- Reijnen R, Foppen R & Meeuwssen H. 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biological Conservation* **75**: 255–260.
- Reijnen R, Foppen R, Terbraak C & Thissen J. 1995. The effects of car traffic on breeding bird populations in woodland. 3. Reduction of density in relation to the proximity of main roads. *Journal of Applied Ecology* **32**: 187–202.
- Rios-Chelen AA, Cuatrecasas-Lima C, Bautista A & Martinez-Gomez M. 2018. No reliable evidence for immediate noise-induced song flexibility in a suboscine. *Urban Ecosystems* **21**: 15–25.
- Rios-Chelen AA, Lee GC & Patricelli GL. 2015. Anthropogenic noise is associated with changes in acoustic but not visual signals in red-winged blackbirds. *Behavioral Ecology and Sociobiology* **69**: 1139–1151.
- Rios-Chelen AA, Quiros-Guerrero E, Gil D & Garcia CM. 2013. Dealing with urban noise: Vermilion Flycatchers sing longer songs in noisier territories. *Behavioral Ecology and Sociobiology* **67**: 145–152.
- Ripmeester EAP, Kok JS, van Rijssel JC & Slabbekoorn H. 2010. Habitat-related birdsong divergence: a multi-level study on the influence of territory density and ambient noise in European Blackbirds. *Behavioral Ecology and Sociobiology* **64**: 409–418.
- Ritschard M, van Oers K, Naguib M & Brumm H. 2012. Song amplitude of rival males modulates the territorial behaviour of Great Tits during the fertile period of their

- mates. *Ethology* **118**: 197–202.
- Rivera-Gutierrez HF, Matthysen E, Adriaensen F & Slabbekoorn H. 2010. Repertoire sharing and song similarity between Great Tit males decline with distance between forest fragments. *Ethology* **116**: 951–960.
- Rivera-Gutierrez HF, Pinxten R & Eens M. 2011. Difficulties when assessing birdsong learning programmes under field conditions: a re-evaluation of song repertoire flexibility in the Great Tit. *Plos One* **6**: e16003.
- Rønning OI. 1972. *Vegetasjonslære*. Universitetsforlaget, Oslo.
- Salaberria C & Gil D. 2010. Increase in song frequency in response to urban noise in the Great Tit *Parus major* as shown by data from the Madrid (Spain) city noise map. *Ardeola* **57**: 3–11.
- Sasvari L & Orell M. 1992. Breeding success in a north and a Central-European population of the Great Tit *Parus major*. *Ornis Scandinavica* **23**: 96–100.
- Singh P & Price TD. 2015. Causes of the latitudinal gradient in birdsong complexity assessed from geographical variation within two Himalayan warbler species. *Ibis* **157**: 511–527.
- Slabbekoorn H. 2013. Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Animal Behaviour* **85**: 1089–1099.
- Slabbekoorn H & den Boer-Visser A. 2006. Cities change the songs of birds. *Current Biology* **16**: 2326–2331.
- Slabbekoorn H, Ellers J & Smith TB. 2002. Birdsong and sound transmission: the benefits of reverberations. *Condor* **104**: 564–573.
- Slabbekoorn H & Peet M. 2003. Birds sing at a higher pitch in urban noise – Great Tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature* **424**: 267–267.
- Slagsvold T, Dale S & Saetre GP. 1994. Dawn singing in the Great Tit (*Parus major*) - mate attraction, mate guarding, or territorial defense. *Behaviour* **131**: 115–138.
- Snijders L, van Oers K & Naguib M. 2017. Sex-specific responses to territorial intrusions in a communication network: Evidence from radio-tagged Great Tits. *Ecology and Evolution* **7**: 918–927.
- SPSS. 2005. *Linear Mixed-Effects Modeling in SPSS: An introduction to the MIXED procedure*. In SPSS Technical report (<https://csass.ucsc.edu/self-study%20courses/SPSSMixed.pdf>). pp. 1–29.
- Stone E. 2000. Separating the noise from the noise: A finding in support of the „Niche Hypothesis,” that birds are influenced by human-induced noise in natural habitats. *Anthrozoos* **13**: 225–231.
- Tietze DT. 2018. *Bird species. How they arise, modify and vanish*. Springer, Cham, Switzerland.
- Tietze DT, Martens J, Fischer BS, Sun YH, Klusmann-Kolb A & Packert M. 2015. Evolution of leaf warbler songs (Aves: Phylloscopidae). *Ecology and Evolution* **5**: 781–798.
- Tolvanen J, Seppanen JT, Monkkonen M, Thomson RL, Ylonen H & Forsman JT. 2018. Interspecific information on predation risk affects nest site choice in a passerine bird. *BMC Evolutionary Biology* **18**: art181.
- Warren PS, Katti M, Ermann M & Brazel A. 2006. Urban bioacoustics: it's not just noise. *Animal Behaviour* **71**: 491–502.
- Weir JT & Wheatcroft D. 2011. A latitudinal gradient in rates of evolution of avian syllable diversity and song length. *Proc R Soc B* **278**: 1713–1720.
- Wilkins MR, Seddon N & Safran RJ. 2013. Evolutionary divergence in acoustic signals: causes and consequences. *Trends in Ecology & Evolution* **28**: 156–166.
- Zbyryt A, Mikula P, Ciach M, Morelli F & Tryjanowski P. 2021. A large-scale survey of bird plumage colour aberrations reveals a collection bias in Internet-mined photographs. *Ibis* **163**: 566–578.
- Zuur AF, Ieno EN & Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**: 3–14.



Ornis Norvegica (ISSN 1892-9737) is a peer-reviewed, online and open access journal publishing original papers in all fields of ornithology. The geographical focus is on Fennoscandia. Descriptive articles documenting bird biology or populations are welcome. Articles dealing with faunistic material should be analytical. Both subscription and publishing are free of charge.

Read articles, submit papers, and more information about Ornis Norvegica at:
<https://boap.uib.no/index.php/ornis/index>