



Unravelling the Stability of Nightingale Song Over Time and Space Using Open, Citizen Science and Shared Data

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Open science approaches enable and facilitate the investigation of many scientific questions in bioacoustics, such as studies on the temporal and spatial evolution of song, as in vocal dialects. In contrast to previous dialect studies, which mostly focused on songbird species with a small repertoire, here we studied the common nightingale (*Luscinia megarhynchos*), a bird species with a complex and large repertoire. To study dialects on the population level in this species, we used recordings from four datasets: an open museum archive, a citizen science platform, a citizen science project, and shared recordings from academic researchers. We conducted the to date largest temporal and geographic dialect study of birdsong including recordings from 1930 to 2019 and from 13 European countries, with a geographical coverage of 2,652 km of linear distance. To examine temporal stability and spatial dialects, a catalog of 1,868 song types of common nightingales was created. Instead of dialects, we found a high degree of stability over time and space in both, the sub-categories of song and in the occurrence of song types. For example, the second most common song type in our datasets occurred over nine decades and across Europe. In our case study, open and citizen science data proved to be equivalent, and in some cases even better, than data shared by an academic research group. Based on our results, we conclude that the combination of diverse and open datasets was particularly useful to study the evolution of song in a bird species with a large repertoire.

Keywords: birdsong, cultural evolution, geographic variation, *Luscinia megarhynchos*, repository, song dialects, vocal learning

INTRODUCTION

Open science practices such as open data (OD), citizen science (CS), and data sharing may open new avenues for answering novel kinds of research questions. Open data are databases and platforms that are freely available to the public and can be reused without copyright restrictions (Kassen, 2013). Acoustic datasets, for example, are increasingly shared publicly both on museum

archives, e.g., the animal sound archive at the Museum für Naturkunde Berlin (MfN)¹, and in open platforms, e.g., Xeno-Canto². Biologists are increasingly using these large open datasets of observations to answer a broad range of questions on evolution and ecology across time and space (Aplin et al., 2021; Dominguez et al., 2021). CS as a concept describes research conducted by non-professional scientists who are not institutionally employed in this field of science (as defined in the Greenbook Citizen Science; Bonn et al., 2017). The use of CS data is rapidly growing, especially in ornithology, and has been successfully used, e.g., for bird monitoring (de Camargo Barbosa et al., 2021), geographical distribution (de Jesus et al., 2021), and population trends (Neate-Clegg et al., 2020). Nevertheless, usage of CS data is not yet well established in ornithology (Weisshaupt et al., 2021) due to a lack of information and thus quality concerns about data availability, data bias, and data generation (Hochachka et al., 2012; Lukyanenko et al., 2016). This quality concern is why CS data are often not made publicly available in the sense of open science. The concerns can be overcome when different datasets are connected, in particular when CS data are used as a complement to fill in gaps (Kirchhoff et al., 2021) or when they are directly compared with data gathered by academic researchers. In an earlier study, we were able to show that citizen scientists made a surprising number of recordings of valid quality when compared to expert recordings and that differences between the recordings were mainly due to the technical quality of the equipment used. Recordings were valid to distinguish songs visually and conduct duration measurements. Frequency measurements showed significant differences depending on the cost, recentness, and brand of the smartphone. Thus, quality is multidimensional and always depends on the research question. In the current study, we conducted a quality dataset comparison based on the same parameters to ensure that open and CS data are considered as sufficiently valuable and are used more often in ornithology. To aid in establishing such a representative case study, we investigated temporal and geographical song variations, so-called dialects, in a bird species.

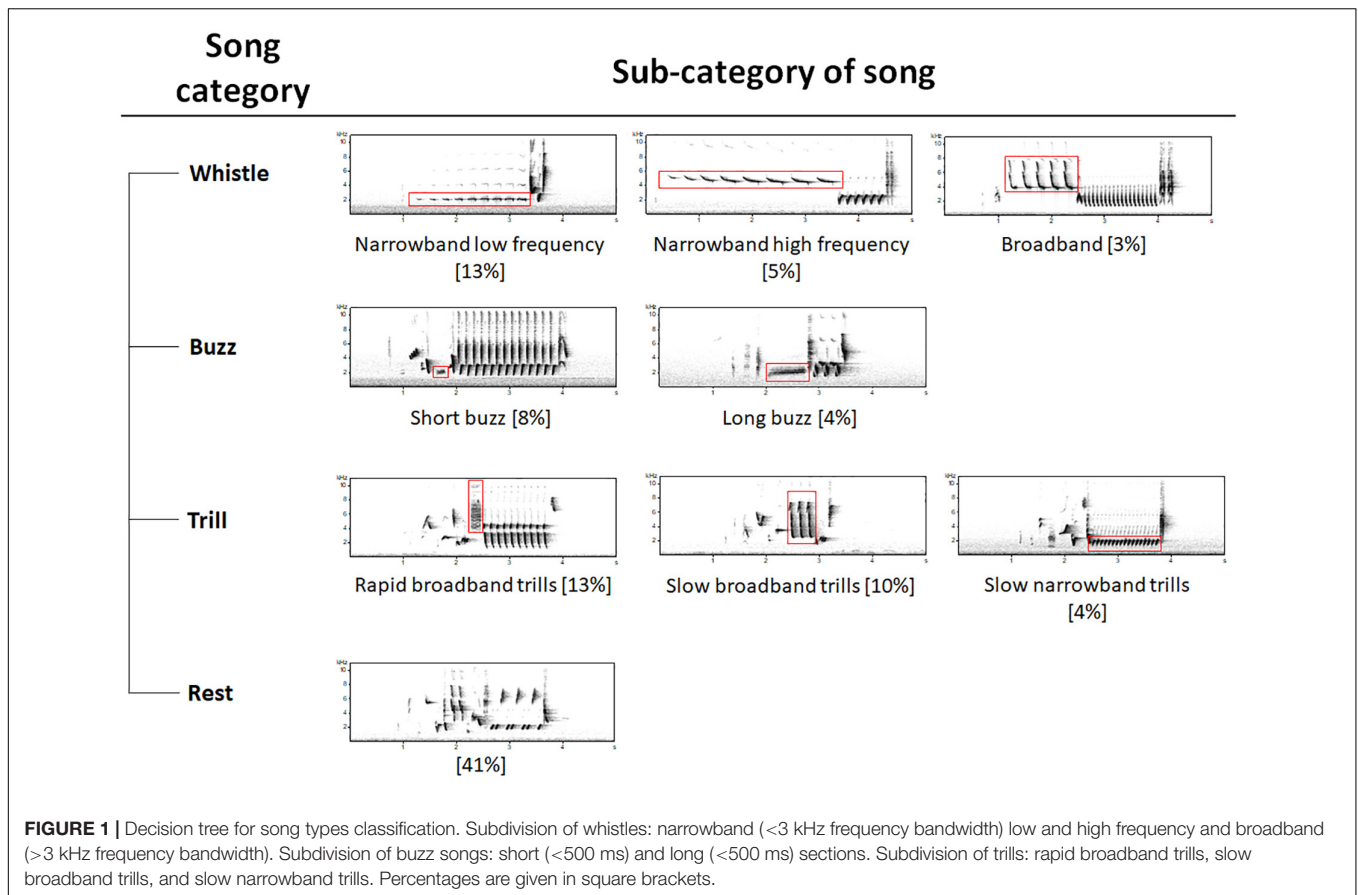
Studies of dialects have historically been based mostly on academic-collected data (in our case shared data) and began as early as (Poulsen, 1958), when Poulsen studied evolutionary processes leading to the formation of dialects, the shape and extent of spatial variation within a species, and the coding of dialects. Dialects have been found with academic-collected data in cetaceans (Sharpe et al., 2019), hummingbirds (Gaunt et al., 1994), parrots (Wright and Dahlin, 2018), suboscine passerines (Kroodsmas et al., 2013), bats (Prat et al., 2017) and with CS data in songbirds (oscine, Searfoss et al., 2020). Song in birds is a sexually selected and culturally transmitted trait that plays a critical role, particularly in breeding ecology as dialects can restrict gene flow among conspecific populations (Baker and Mewaldt, 1978) or contribute to reproductive isolation and speciation resulting in ring species (Irwin et al., 2001). In the well-studied, mostly temperate model species, males sing to defend their territory and attract females (Catchpole and Slater, 2008).

Songbirds acquire their song mainly through social learning via cultural imprinting. In this process, young males learn their song from their parents or neighbors and pass those songs onto the next generation (Mennill et al., 2018). This process can lead to copying errors and modifications over time and space, resulting in a cultural evolution of song (Lynch, 1996). Sexual selection, cultural drift, environment, and population adaptation (immigration, emigration) influence whether song types are particularly common or rare in individual songs and populations (Derryberry et al., 2011). A song type is a unique sequence of elements with defined frequencies and durations, as described by Gil and Gahr (2002). If song types are beneficial to individuals in terms of environmental adaptation, female choice – or their own fitness – some songs types persist over time (Lynch, 1996). Unbeneficial song types can be loosed or modified, which lead to geographic variation that may evolve into distinct, local dialects over time (Beecher and Brenowitz, 2005). Local dialects reduce song variation at the microgeographic level compared to the macrogeographic level, resulting in greater differences between populations than within populations (Catchpole and Slater, 2008). Investigating dialects over time and space allows insight into the processes of song evolution (Rendell and Whitehead, 2005) and improves the understanding of songs as well as repertoires and thus vocal learning (Pozzi et al., 2010). Previous dialect studies have increasingly benefited from the use of open databases (Wright and Dahlin, 2018) and CS recordings (Diblíková et al., 2019). Due to the internet and GPS-based app development (Dickinson et al., 2012), these studies generated considerable data on a spatial and temporal scale that would be unachievable for traditional scientific studies due to financial or logistical constraints (Diblíková et al., 2019). These studies showed that songs and parts of them remain stable for up to three decades (Nelson et al., 2004) or change geographically especially in bird species with small repertoires, and typically with one to three song types (Diblíková et al., 2019; Searfoss et al., 2020). Nevertheless, it is not yet known how the song or parts of it evolve over a century or Europe-wide across the entire breeding range and in a bird species with a large repertoire.

In our study, we examined the common nightingale (*Luscinia megarhynchos*), a species with approximately 190 song types (Hultsch and Todt, 1982) and a Europe-wide breeding range (from the Mediterranean to Central Asia in the East and Central Europe in the North; Glutz von Blotzheim, 1988). The nightingale is particularly interesting for studies on song dialects due to its complex and well-studied song behavior in the field (e.g., Kiefer et al., 2006) and in the laboratory (e.g., Hultsch and Todt, 1996). Males are territorial, return to their natal breeding area, and have been found to also occupy the same territory in consecutive years (Roth and Amrhein, 2010). Songs can be classified into four song categories (whistle, buzz, trill, and so-called “other songs,” **Figure 1**) as well as song types which form the song repertoire (doctoral thesis Hultsch, 1980; unpublished data). Nightingale males, as so-called open-ended learners, are among the bird species in which 1-year-old males can significantly expand and adjust their repertoire for the following breeding season, but not thereafter (Kipper et al., 2004). In this process, song types are learned in a very stereotypical way (Hultsch et al., 1999), which

¹<https://www.tierstimmenarchiv.de/>

²<https://xeno-canto.org/>



has the capacity to make the song repertoire very diverse with many individual song type variations (Landgraf et al., 2015). These different song types are not repeated directly, but rather after a variety of other song types, with some shared commonly and others rarely within and between individuals (Hultsch and Todt, 1989). Earlier studies have already shown that neighboring nightingales in intermediate distances share a higher proportion of songs than close or distant ones (Hultsch and Todt, 1981) due to song type adjustment to the breeding population (Kiefer et al., 2010, 2014). Based on knowledge of song ontogeny and migration behavior, temporally stable and geographically variable nightingale song can be expected and would be consistent with previous studies. Weiss (2012; unpublished data) noted in his doctoral thesis that dialects are most likely coded in the number of times a song type appears (relative frequency). Schehka (2004) found in her master thesis that common song types have been proven to be stable in their occurrence over two decades and in two countries, while she did not study rare song types. Thus, several lines of evidence suggest that stability and dialects may be occurring on a larger scale, although their extent has not been fully investigated yet. We addressed this question in our study by examining the stability (occurrence of common and rare song types), and dialects (relative frequency) on an expanded temporal (almost a century) and geographical (whole Europe) scale. Because certain parts of songs (thereafter defined as sub-categories of song) showed stability in some and coded for

dialects in other species with a small repertoire, we investigated their function in the large repertoire of the nightingale. OD and CS data approaches have been used successfully for dialect research in other species with few song types (Wright and Dahlin, 2018; Diblíková et al., 2019), but never before in a songbird with so many song types, such as the nightingale. Therefore, we examined whether the datasets showed different results for the sub-categories of song, the occurrence or relative frequency of common song types to assess their comparability and derive their respective usefulness.

To investigate the potential for new avenues for research, we specifically addressed two biological and one technical hypothesis: (1) Common song types occur in a stable manner over nearly a century in the nightingale song (H1: stability). Since stable common song types have previously been found over two decades in the nightingale, we predicted stability over several decades, as has been detected in other species. (2) The relative frequency of common song types is encoded for dialects in nightingales across Europe (H2: dialects). As the relative song type frequency has been shown to differ in the nightingale between two neighboring countries, we predicted that such variance occurs also across the entire breeding range of the nightingale. (3) The sub-categories of song, occurrence, and relative frequency do not differ between the datasets (H3: datasets). Since OD, CS, and shared data have been used successfully for dialect research in other species and CS

recordings were determined to be as valid as scientific recordings in an earlier comparison, we expected that all datasets used will be appropriate for nightingale dialect research.

MATERIALS AND METHODS

The Nightingale Song as a Model in Song Research

The nightingale is a recognized model species in song research due to its clearly structured song with durations of about 2–4 s alternating with silent intervals (pauses) of similar length (Hultsch, 1980; unpublished data). The basal unit is an element with a characteristic frequency (bandwidth) and duration, containing pauses less than 10 ms. Up to four elements are grouped together to form syllables which are separated by pauses of 10 ms and produced once or several times repeated in a stereotypic order, form phrases. These are grouped into four sections (α , β , γ , and Ω) which can be characterized by analyzing element features and repetition rate (Hultsch, 1980; unpublished data; **Figure 1**). Male nightingales can produce a variable number of distinct song types whereas different individual birds can sing the same song type with minor variations (between them, or from rendition to rendition), resulting in extraordinarily large song repertoires (on average 190 with a maximum of 250 different song types; e.g., Hultsch and Todt, 1982; Kipper et al., 2004). As it is therefore challenging to study the song and with regard to the work economy, we focused on 20 song types (approx. 10% of the song types of a nightingale repertoire, **Supplementary Figure 1**). For this species, it is a standard procedure (e.g., Kipper et al., 2015) and has also been used in a previous dialect study of the nightingale due to the complex song (Schehka, 2004; unpublished data). We examined the ten most common and the ten rarest song types (occurred only once) from Berlin-Brandenburg within all datasets and across years. As there were 276 rare song types we selected ten of them randomly. Using these 20 song types (ten common, ten rare ones with Berlin-Brandenburg as a reference point) we analyzed their geographical occurrence across Europe. The ten most common song types were used for the temporal and dataset occurrence analysis and the relative frequency estimation for time, space and datasets.

Databases

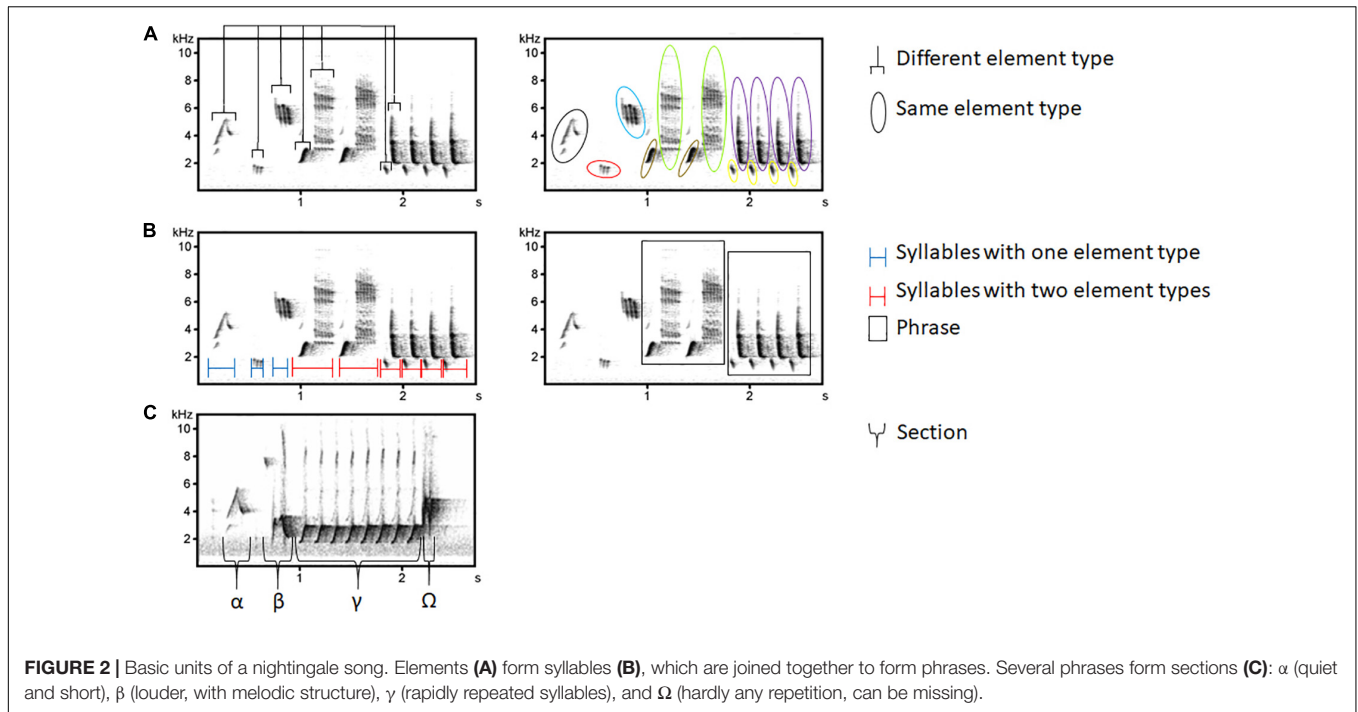
To unravel the potential of OD, CS, and data sharing, we used and compared four datasets (**Figure 3**): one open archive, two CS datasets, and one shared dataset. In total, we analyzed 14,140 nightingale songs. Since the length as well as the recording quality varies greatly, songs are a better measure to indicate the amount of data material than recording numbers. No recording originated from more than one dataset. Recording standards varied, depending on the species, research question, and context. For studies on individual song differences in the nightingale, 1-h nocturnal recordings are the standard (Kiefer et al., 2014), as they contain the most songs as well as no disturbing background noise in terms of other singing birds (bachelor thesis Jäckel, 2013; unpublished data). Only the shared recordings were standardized. The other datasets were unstandardized in terms

of technique (smartphones to professional equipment), time (day and night), location (Europe-wide), and durations (few seconds to 90 min). However, standardized recordings were not required for our study, as we were working on the population rather than the individual level. Individual differences are used to define signature and not geographical variations. We cannot completely rule out the possibility that certain individuals were recorded repeatedly and therefore their songs occur multiple times in our dataset, in particular this is the case for the citizen science data. However, based on the GPS data we assume that the vast majority of recordings were not from a few individuals, but that the recordings were well distributed in space and time. To emphasize that we are not making statements about individuals, we worked at the population level.

We used the open animal sound archive of the MfN (hereinafter abbreviated as ASA) which contained recordings from the 1930s until 2015 of which we examined 3,262 songs from Germany. These recordings were generated by different experts with different recording devices (sampling frequency: 96 kHz; resolution: 16 bit). The data were distributed differently over the decades, with a significant decrease from 2006 onward. We analyzed 3,833 songs from a nightingale citizen science project (project name: “Forschungsfall Nachtigall,” hereinafter abbreviated as FFN; eng. “nightingale citizen science project”), led by a team of academic researchers at the MfN. These recordings were generated with diverse smartphones (sampling frequency: 44.1 kHz; resolution: 16 bit) within 2018 and 2019 mainly in Berlin. Additionally, we examined 4,751 songs from the CS website Xeno-Canto of 13 countries and spanning over 26 years. These recordings were generated by both laypeople and experts, using a wide range of technology (sampling frequency: 8–48 kHz; resolution: 16 bit). The shared dataset of 2,294 songs from Berlin was generated by academic researchers (hereinafter abbreviated as AR) in 2018 and 2019 by students of Freie Universität Berlin (Berlin, Germany) and staff of the FFN. Recordings were generated with Sennheiser ME66/K6 directional microphones (Georgsmarienhütte, Germany) connected to a Tascam Dr-40 4-Track Portable Digital Recorder or a Marantz solid-state recorder PMD660 as well as Zoom H2n recorders (sampling frequency: 44.1 kHz; resolution: 16 bit).

A European Nightingale Song Type Catalog

The high precision of song learning, copying, and delivering in male nightingales within and between individuals allows for a reliable assignment of a song to the same song type (Hultsch et al., 1999). We used Avisoft SASLab Pro 5.2 (R. Specht, Berlin, Germany) for visual inspection of songs (sampling rate = 22.05 kHz, FFT = 1024 points, Hamming-Window, overlap 93.75%). As Avisoft can only open WAV files, the MP3 and m4a recordings were converted into WAV files by using the program WaveLab 7. We started our cataloging process with recordings from Berlin-Brandenburg and extended across Germany and Europe. During the last 2 years, a single person (DJ) visually compared songs using spectrograms with catalog song types and categorized a song as either known or new. We did a self-check



	Open Science	Citizen Science		Shared data
Data sources	Animal sound archive	Xeno-Canto	„Forschungsfall Nachtigall“	Academic researchers
Specification of the recordings				
Devices	Professional equipment	Professional equipment	Smartphones	Professional equipment
Maximum duration (min)	unlimited	unlimited	2	60
Mean duration (min)	24 (± 15)	1 (± 3)	1 (± 0.4)	60 (± 0)
Recording person	trained	untrained & trained	untrained	trained
Number of recording persons	28	342	>3,000	9
Raw data				
Number of songs	3,262	4,751	3,833	2,294
Number of song types	795	1,273	302	361
Number of countries	1	14	4	1
Number of years	88	26	2	2

FIGURE 3 | Overview of the data material for open science [animal sound archive (ASA)], citizen science [Xeno-Canto and “Forschungsfall Nachtigall” (FFN)] and shared data [academic researcher (AR)]. Information was separated into specification of the recordings and raw data.

at the beginning to evaluate the accuracy of the cataloged song types. In this cataloging process, comparable to the nightingale song type catalog of Hultsch and Todt (1981) and Kipper et al. (2004), we based the definition of a song type on an identical γ -section. But our analysis differed from their previous catalog: (a) As we worked with different types of recordings (unknown individuals), we defined variations of a song type as all differences in the elements in the α , β , and in the Ω -section (Figure 2). Variations in the previous catalog occurred when more than three of ten elements (80% of the song type) differed in the α or β

section. Variations are thus minor modifications of a song type that do not occur in the repetitive γ -section. We therefore based the structure within our song type catalog on the γ -section since any differences in that section were used to define a new song type. (b) We added all newly found song types to the catalog. For the previous catalog, which was based on 1-h song recordings of individual known nightingales, it was necessary that song types had to be sung at least twice by the same male in the same recording to be included. (c) We created our catalog on a basis of recordings across European datasets without any knowledge of

the individual. Doing so, we created a European song type catalog on the population level.

Sub-Categories of Song Classification

We established previously that recordings made with qualitatively and technically different recording devices presented significantly different acoustic parameters in subsequent measurements. Therefore, we based the classification of sub-categories of song on visually distinguishable parameters, i.e., frequency ranges, durations, pauses, and element rates – and not on measuring frequencies. Sub-categories of song were extended divisions of the known four song categories of the nightingale: whistles, buzzes, trills, and “other songs” (Figure 1; Hultsch, 1980; unpublished data). “Other songs” were not further subdivided. Whistle, buzz and trill elements occur in the γ -section. Whistle elements never occur with buzz elements in the same song type simultaneously. It is possible that whistle or buzz elements are followed by trill elements in different sections, whereas these are no trill songs.

Whistles have been shown to have frequency-dependent functions (Hultsch, 1980; unpublished data) and are used for female attraction (Naguib et al., 2002). On this basis, we classified whistles according to the frequency bandwidth of the last whistle element into narrowband (<3 kHz) and broadband (>3 kHz) ones. We divided the narrowband ones corresponding to the frequency of the last whistle element into low (<4 kHz) and high (>4 kHz) whistles. Buzz songs have been found to indicate the quality of a male by the length of the buzz section (Weiss et al., 2012). We subdivided the buzz songs into ones with short (<500 ms) and long (>500 ms) sections. The relationship between frequency bandwidth and trill rate has been demonstrated to serve as an aggressive signal in nightingales (Kunc et al., 2006). In some bird species, this relationship has been found to indicate the quality of a male to females (Podós, 1996). Based on this finding, we divided the trills into rapid broadband (bandwidth of >9 kHz and an element repetition rate without visible pauses between the trills), slow broadband (bandwidth of >9 kHz and element repetition rate with visible pauses between the trills), and slow narrowband trills (bandwidth <6 kHz and element repetition rate with visible pauses between the trills).

Comparison of Time Periods

We specified four time periods (TP) for the temporal analysis. TP1 was defined by us as the 1930s, followed by TP2 (1960–1980), TP3 (1981–2000), and TP4 (2001–2019). As the recordings were not evenly distributed over time and some years were missing, we had to combine two decades as one TP (Figure 4A). See for an overview of the songs per TP and datasets in Supplementary Table 1.

Comparison of Geographical Regions

For the geographical analysis, we selected the region Berlin-Brandenburg as a reference for a location since the majority of our recordings (58%) were generated there and both, the FFN and the AR recordings, largely originated from this region (99–100%). We did not have GPS tags of a large amount of the recordings for the countries Italy, France, Spain, and Portugal, which did not

allow for a statistical method to classify the regions. We merely had the information about the respective countries but did refrain from a comparison based on national borders. Thus, due to the missing metadata, we based the geographic distribution on the approximate estimated distance from Berlin-Brandenburg and defined five geographical regions (Figure 5A). An overview of the songs per region separated according to the datasets is available in Supplementary Table 2.

Comparison of Different Databases

In order to compare the different datasets, we chose the same time period (TP4: 2001–2019) and region (Berlin-Brandenburg) to exclude temporal and regional differences in the analysis. We chose this period because the last recordings from the ASA were from 2015. In addition, the AR and FFN recordings were generated in 2018 and 2019. We thus had sufficient recordings to study and compare data from all datasets (AR: 2,294 songs; ASA: 1,669 songs; FFN: 3,366 songs; Xeno-Canto: 99 songs; Figure 6A).

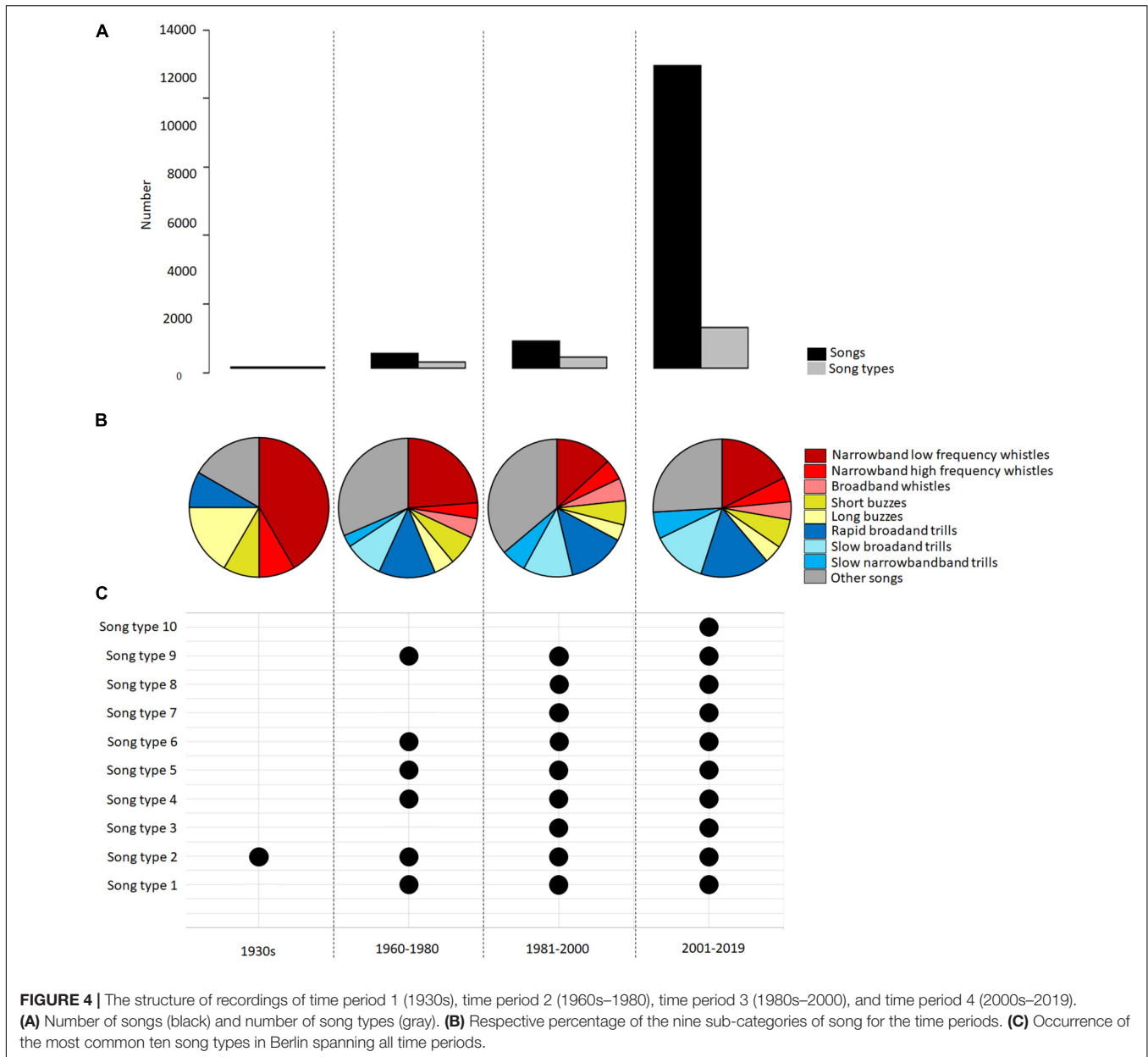
Statistical Analyses

For the occurrence analysis of a given song type, we recorded whether it was present or absent in the recordings that we analyzed over time, space or dataset. We defined the relative frequency from the number of times a song type appears divided by the total number of songs. Two one-sided tests (TOST) were used to test for the effects of time, space, and datasets for sub-categories of song and the relative frequency of song types. We set the upper and lower equivalence boundary at 0.5 and the statistical significance at $p \leq 0.05$. All statistical analyses were performed using R version 4.0.0 (R-Team, 2020; unpublished data).

RESULTS

European Song Type Catalog

Based on 14,140 songs from four datasets, we created a European nightingale song type catalog at the population level, which currently contains 1,868 different song types. As of September 2021, the catalog comprises 20% whistles, 12% buzz, 27% trills, and 41% so-called “other songs.” The nine sub-categories of song were significantly equivalent between the datasets in their percentages (TOST test: equivalent p -values of <0.01). The occurrences of song types differed among the four datasets. 78% of songs types appeared in only one of the datasets, 9% of songs types were found in two of the datasets, 5% of songs types occurred in three datasets and 8% of songs types were in all four datasets. Song types occurred with different frequencies in all datasets (1 \times : 56%; $\leq 10\times$: 30%; >100 \times : 1%). The rate of new song types that have not yet been sung (song type diversity) was different between the datasets (AR: each sixth song; ASA: each fourth song; FFN: each thirteenth song; Xeno-Canto: each fourth song). The agreement between the song types varied (highest between AR and FFN: 61%; lowest between Xeno-Canto and ASA: 26%; Supplementary Table 3).



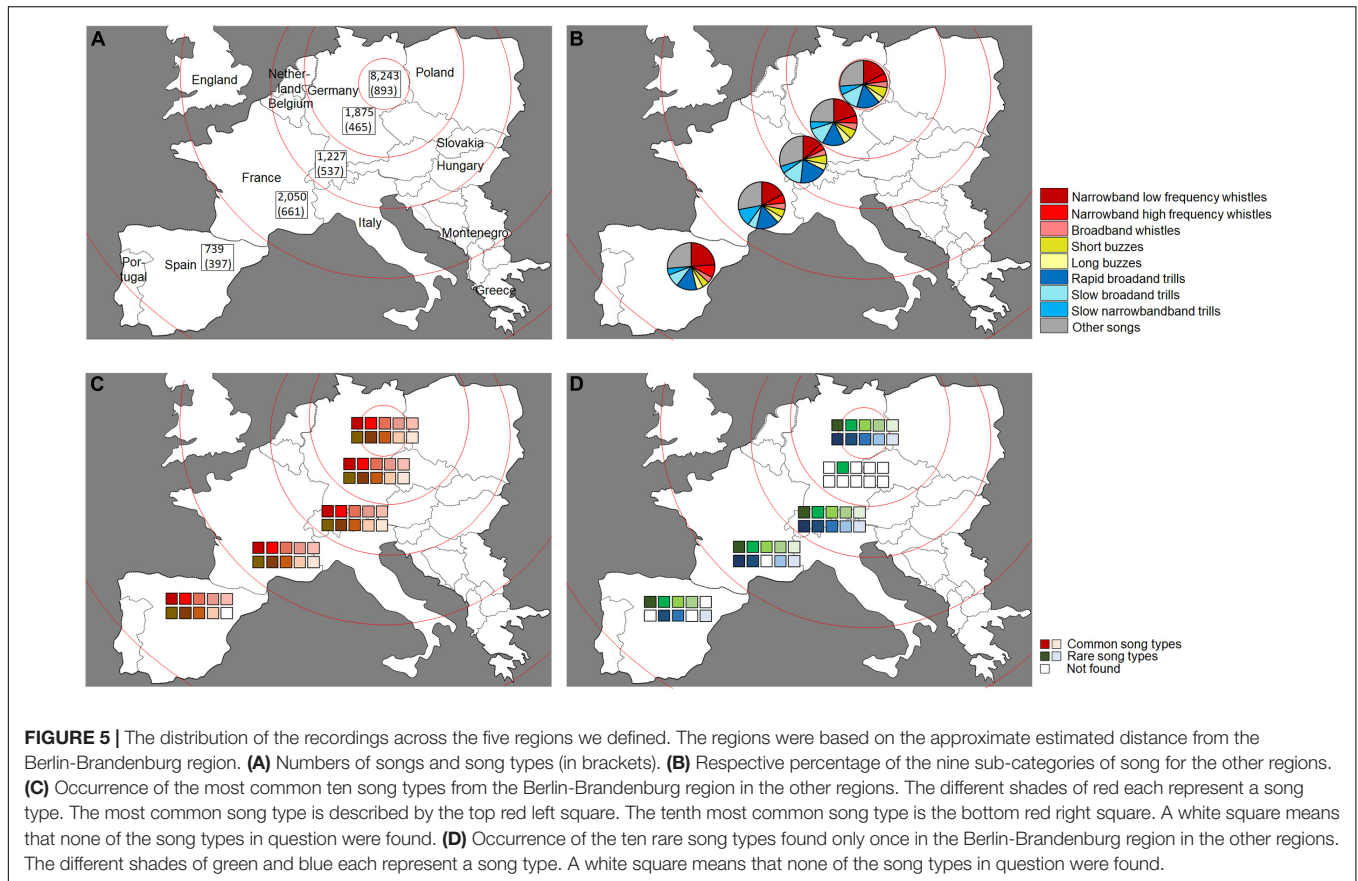
Temporal Comparison of Nightingale Song

When comparing the sample years between 1930 and 2019 among all datasets, we detected that the nine sub-categories of song were distributed in a stable way with similar percentages over time (TOST test: equivalent *p*-values of <0.01). In most time periods, the narrowband low-frequency whistles, the rapid broadband trills, and the “other songs” accounted for the largest percentage of the nine sub-categories of song (Figure 4B and Supplementary Table 4). An analysis with regard to song type stability showed that the second most common song type in our dataset – a narrowband low-frequency whistle – occurred in all time periods. Six common song types were found in the recordings from the 60s until 2019 (Figure 4C). An analysis with

regard to the relative frequency of the ten most common song types revealed that they accounted for 2% of the total number of songs and were significantly equivalent between the time periods (TOST test: equivalent *p*-values of <0.01).

Geographical Comparison of Nightingale Song

A comparison between the five geographic regions in all datasets showed a stable and similar distribution in the percentage of the nine sub-categories of song over space (TOST test: equivalent *p*-values of <0.01). The highest percentage of the nine sub-categories of song was accounted for by the low-frequency narrowband whistles, the rapid broadband trills and the “other songs” in all regions (Figure 5B and



Supplementary Table 5). An analysis with regard to the stability of the ten most common song types revealed that nine of them were found in four of our geographic regions (Figure 5C). Six of the ten rare song types occurred in four regions (Figure 5D). An analysis with regard to the relative frequency of the ten most common song types showed that they accounted for 2% of the total number of songs and were significantly equivalent between the regions (TOST test: equivalent *p*-values of <0.01).

Comparison of Nightingale Song Among the Four Different Datasets

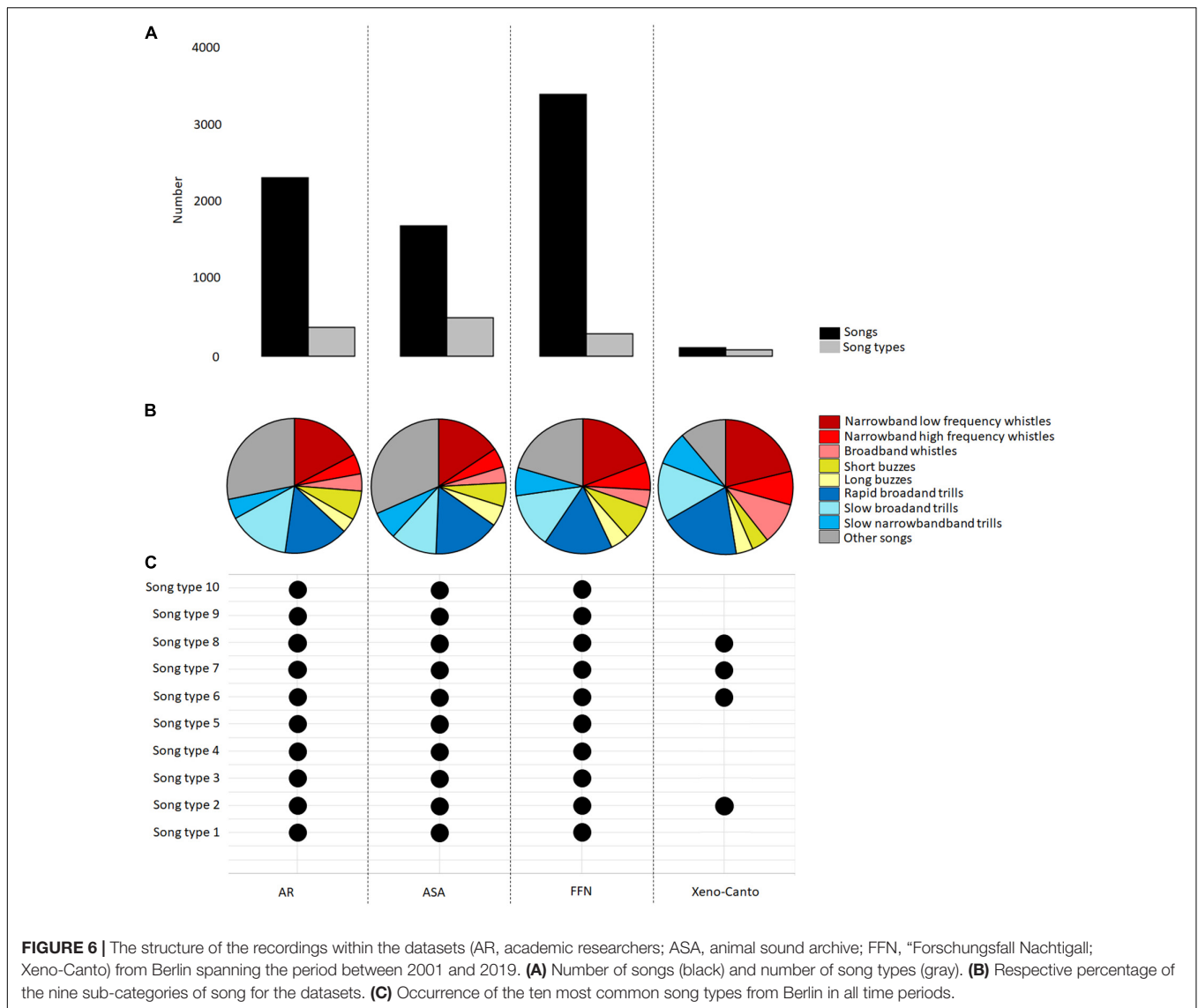
We found an equal distribution of the nine sub-categories of song when comparing the four datasets in the time between 2001 and 2019 from Berlin-Brandenburg (TOST test: equivalent *p*-values of <0.01). The low-frequency whistles had the highest percentage, followed by the rapid broadband trills and “other songs” (Figure 6B and Supplementary Table 6). Concerning the ten most common song types, four of them occurred in all datasets (Figure 6C), six of them occurred in the AR, ASA, and FFN recordings. An analysis with regard to the relative frequency of the ten most common song types revealed that they accounted for 3% of the total number of songs and were significantly equivalent between the datasets (TOST test: equivalent *p*-values of <0.01).

DISCUSSION

The aim of this study was to investigate whether nightingale song is stable in terms of song type occurrence over nearly a century and whether song dialects are found in the relative frequency of song types across Europe. We also examined if sub-categories of song codes for stability or dialects. Additionally, we investigated if open, citizen science and shared data are an advantageous complement for dialect studies in a bird species with a large repertoire. Our study encompassed a period twice as large as previous studies (e.g., Grant and Grant, 1996) with recordings from the 1930s until 2019 and covered a linear geographic range of 2,652 km across 13 European countries, twice as large as previous studies (e.g., Weiss, 2012; unpublished data). In the following, we will evaluate the results from the biological (temporal stability and spatial dialects) and the technical (comparison of different datasets) perspectives.

Vocal Dialect Research Across Time and Space

Our European population-based nightingale song type catalog was three times larger than a previous one (623 song types; Weiss et al., 2014), which included songs of 271 individual nightingale males from a Berlin and 272 from a Brandenburg population. In addition, the catalogs differed in two more respects. First, we included all song types, instead of only



those that appeared at least twice because otherwise that would have resulted in the loss of 1,048 song types. Second, in the definition of new song types: any differences in γ -section (our study) vs. less than 80% similarity or differences in more than three of ten elements in the α - and β -section (Weiss et al., 2014). However, we would like to emphasize that even if the total number of song types varies between the different catalogs, the results should remain unaffected. This notion is supported by the number of song types for the Berlin-Brandenburg region in two populations (623, Weiss et al., 2014) compared to multiple populations (893, our method).

Despite our large song type catalog, we found, for the first time, stability both in time (nearly a century) and space (geographical area — Europe) within the percentage of sub-categories of song and the occurrence of song types (common and rare) in the song of a bird species with a

large repertoire. The stability of two frequent sub-categories of song could be explained by the fact that they may indicate the quality of a male, as low-frequency whistles and rapid broadband trills are difficult to produce as has been shown in other species (Podos, 1996; Kirschel et al., 2009), and degrade less in the nightingale habitat (Wiley and Richards, 1978). Thus, these sub-categories of song indicate stability over time and space in bird species with large (the nightingale) and small repertoires (Nelson et al., 2004) and cetaceans (Deecke et al., 2000). Temporal stability in the occurrence of song types have also been found in songbird species with a small repertoire (Grant and Grant, 1996), hummingbirds (González and Ornelas, 2009), parrots (Wright et al., 2008) and in cetaceans (Rekdahl et al., 2013), where the most common vocalizations were likewise stable. Although geographic persistence of certain song types has been noted in songbirds (Searfoss et al., 2020) and parrots (Wright et al., 2008), suggesting an important function in animal

communication, we expected temporal stability and spatial drift: (a) Nightingales have been shown to adapt their song to the population from the first to the second breeding season (Kiefer et al., 2010, 2014). (b) Nightingales have been demonstrated to share song types among males of the same population to facilitate communication during interactions between males (Todt and Naguib, 2000). (c) Different song types are performed with different frequencies, while those shared with neighboring males are common (Hultsch, 1980; unpublished data). The stable occurrence of common and rare song types detected in our large dataset is consistent with previous playback experiments (Weiss, 2012; unpublished data). Moreover, this stability seems to be consistent with the nightingale behavior in the wintering grounds (Glutz von Blotzheim, 1988). Spatially separated nightingales probably interact on wintering grounds, which could lead to adaptation and stability of song types. These stable song types could have positive effects (adaptation to the environment, choice of female) and an important communicative function in social interactions, such as in cetaceans (Rekdahl et al., 2013). All this could have led to the fact that the song characteristics we studied were stable across time and space. Future studies should investigate exactly which and why these stable song types exist in nightingale song, and how they mediate communication.

In contrast to our findings on the stability of nightingale song, we observed no evidence of song dialects in the relative frequency of the ten most common song types across Europe. As Weiss (2012; unpublished data) found differences in the relative frequency of song types between populations from Berlin, Brandenburg, and France, we expected the same for Europe in general. However, the relative frequency of common song types was so low that no geographical differences could be inferred. This low relative frequency could be related to the size of our song type catalog but not to the datasets used, as they showed the same results. However, as the exact relative frequency of song types of a male can only be determined after approximately 1 h (533 songs; Kipper et al., 2004), we suggest that it is not the relative frequency of a single song type that codes for dialects, but the composition of song type delivery of a bird, i.e., repertoire or syntax (Weiss, 2012; unpublished data). This has already been suggested for orcas (Riesch et al., 2006; unpublished data) and is in line with previous bird studies showing that even species with a large repertoire recognize foreign males from short songs without the need to listen to the complete repertoire (e.g., Jaška et al., 2015; Moser-Purdy and Mennill, 2016). Since nightingales sing with immediate variety, i.e., the same song type is not sung repeatedly, but only after a certain number of songs (Hultsch and Todt, 1989), this pattern allows them to hear several song types in a short time – and thus may enable nightingales to determine whether a singer is a resident or a stranger. This result is indeed consistent with studies suggesting that song dialects are unlikely to emerge in species with a large vocal repertoire (Goodfellow and Slater, 1986; Lachlan et al., 2016; Tchernichovski et al., 2017), such as the nightingale. However, we need to stress that we in fact only looked at a rather small part of the nightingale song type catalog determined in our case study. Thus, future studies could extend the analysis to examine if potentially other common or rare song types code for dialects.

Combining Datasets for Research Over Time and Space

We evaluated OD, CS, and shared data for dialect research over time and space in direct comparison of sub-categories of song, as well as the occurrence and relative frequency of the ten most common song types in nightingale song. The similarity in the three most frequent sub-categories of song and variations in the other six sub-categories of song probably resulted from some song types occurring in only one dataset, leading to different song type diversities and thus percentage distribution. Because all ten common song types were found in the datasets, except Xeno-Canto, we suspect that the absence of the common song types was due to the number of analyzed songs. Since these 99 Xeno-Canto songs were only sufficient for finding four common song types, about three times the amount of songs is needed for a valid analysis. We showed that the datasets are not different *per se*, but our evaluation was influenced by other aspects.

The differences between the datasets were evident in their temporal and spatial validity for our analysis, as all exhibited either a temporal or spatial bias. Our temporal analysis was mainly conducted with the OD and the CS (especially Xeno-Canto) recordings. The spatial analysis was mainly possible with the CS recordings as these had the largest spatial distribution and the most metadata, since these were generated with an app (FFN) and Xeno-Canto requires a minimum of metadata for the recordings (Vellinga and Planqué, 2015). CS projects can provide more data with a greater geographic coverage than academic researchers alone, which are limited in number of simultaneously generated recordings due to the (mostly) stationary location and the restricted availability of (expensive) equipment (e.g., Vellinga and Planqué, 2015; Steen et al., 2021). The shared data were the least suited for our temporal and geographic analysis as they were only from 2 years from Berlin. The importance of the geographic distribution of the recordings was evident in two ways: First, song type diversity was mainly affected by the spatial distribution of the recordings and not by the number of songs and thus the size of the dataset nor the duration or the time of the recording as no song types only occur at night or day (Jäckel, 2013; unpublished data). Second, the degree of concordance of song types in each dataset was also influenced by spatial distribution, with datasets from the same region (e.g., AR and FFN) accounting for the greatest share. We conclude that to study song stability and dialects (1) the recording location is more important than recording length and that (2) many short, non-standardized OD and CS recordings may achieve the same diversity of song types within a dataset as long, standardized professional recordings. Thus, for our study using the nightingale as an example, standardized recordings were not required in terms of technology (professional equipment), time (nocturnal song), duration (1 h), or great experience of the recordist.

Our study showed that even if longer recordings would have been helpful, considering the large repertoire of the nightingale, it was more critical for our temporal and spatial analysis to have access to diverse datasets. To make access also possible for future nightingale researchers, we are in the process of making the recordings from the FFN online available in an open archive

at the MfN. Currently only half of the academic researchers publish their data in open archives (Tenopir et al., 2011), as such access is not encouraged widely, which reduces the opportunities for reuse (Mills et al., 2015; Federer, 2020). Missing open science practices are particularly disadvantageous for evolution and ecology research, where datasets from longitudinal studies contribute greatly to scientific understanding but are expensive and time-consuming (Mills et al., 2015; Hughes et al., 2017). We would therefore like to encourage more song recordings to be made publicly available with sufficient metadata so that they can be effectively used in future research. Open science, and thus the availability of diverse datasets, allowed us to conduct the largest temporal and geographic study of song evolution to date. By directly comparing the datasets, we have shown that OD and CS recordings are well suited – and in some cases better suited – for studying song variation in bird species with a large repertoire than data collected by an academic research group, because they were collected over a shorter period of time and in a much smaller geographic range. Therefore, we recommend that OD and CS datasets should be used more frequently in ornithology and that song recordings should be openly accessible. Given that each dataset has different advantages and disadvantages, we further recommend combining diverse datasets for dialect research in bird species with a large repertoire.

CONCLUSION

In our study, we found the song of common nightingales to be stable over time and space. We did not detect evidence of dialects. However, the nightingale has a highly sophisticated syntax and a complex song, only a small part of which we studied, so further analysis is needed to rule out the absence or presence of dialects. Our results showed that non-standardized OD and CS recordings offer the potential to support ornithology and in particular dialect research. The general quality concerns about OD and CS could not be confirmed in our study. Based on our findings, when studying a bird species with a large repertoire such as the nightingale, we recommend combining different and diverse datasets as quality is multidimensional and always depends on the research question. As more and more (CS) recordings are currently being made available on open platforms (Sanderson et al., 2021; unpublished data), our study is of great use to increase trust in them. We hope to encourage fellow bird enthusiasts to share their song recordings in open repositories and promote the use of these data to the scientific community.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval were not required for the animal study because, in Germany, permission from an ethics committee is not required for such research questions.

AUTHOR CONTRIBUTIONS

DJ, KM, and SV-H wrote the concept and design of the study and analyzed and interpreted the data. DJ and UB performed the statistical analysis and designed the figures. DJ wrote the first draft of the manuscript. KM, GL, and SV-H revised the manuscript. All authors contributed to the manuscript and revised, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.778610/full#supplementary-material>

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