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Four decades later: The highly conserved repertoire of song types in chaffinch (*Fringilla coelebs*)

Vladimir Ivanitskii [a,*], Irina Marova [a], Irina Samsonova [a], Ilya Volodin [a,b,1], Elena Volodina [a,b,2]

[a] Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobievy Gory, 1/12, Moscow 119234, Russia
[b] Department of Behaviour and Behavioural Ecology, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospect, 33, Moscow 119071, Russia

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ABSTRACT

The long-term stability of culturally transmitted traits like bird song has attracted much attention from researchers; however, it remains insufficiently studied up to the present time. This study investigates, by using spectrographic analysis, whether the repertoire of song types recorded at the same locality is persistent at short terms (of four years) and at long terms (of 38 years) in a migratory European continental population of chaffinches. The population song type repertoires recorded in 1978 and 1982 were only slightly different, thus indicating the high repertoire persistence within a few years. There were more differences between repertoires recorded in 1982 and 2020. In total, eight of the 29 song types (28 %) identified in 1982 were not found in 2020, and 5 of the 26 song types (19 %) discovered in 2020 were completely new compared to 1982. All the other song types recorded in 2020 were similar to those recorded in 1982. The frequency of use of these song types in 1982 and 2020 was also similar. By 2020, mainly those song types had disappeared from the population repertoire, which in 1982 were performed by a limited number of males. These data suggest a high long-term persistence of repertoire of song types in male song of a migratory continental population. This long-term stability of the population repertoire was maintained despite significant changes in the habitat structure caused by a massive expansion of bark beetles in 2010–2014.

1. Introduction

Many oscines are known to acquire their songs through a process of cultural transmission whereby individuals learn songs by hearing those of conspecifics during early development (Catchpole and Slater, 2008; Beecher, 2017; Aplin, 2019). One important consequence of this learning process is spatial and temporal variation in songs (Krebs and Kroodsma, 1980; Williams, 2021).

The temporal variability of bird song attracts a lot of attention from researchers. In particular, it was found that the rate of change in population repertoires varies significantly over the years in different species (Podos and Warren, 2007) or even in different populations of the same species (Luther and Baptista, 2010; O'Loghlen et al., 2013). Different components of population repertoires (syllables or song types) change at a different rate: some are performed in a given territory for many years, others change significantly over the same period, and others are completely excluded from the repertoire (Ince et al., 1980; Nelson et al., 2004; Goodale and Podos, 2010; Williams et al., 2013).

A number of studies indicate that the individual and population repertoires of songbirds can change very quickly, even within a few years (Williams, 2021). This primarily applies to "open-ended learners", i.e., those that can learn to sing new songs, not only in their youth, but also in adulthood. For example, in yellow-rumped cacique (*Cacicus cela*), prone to vocal mimicry, 78 % of the repertoire is changed per year (Jaramillo and Burke, 1999). A significant interannual rotation of song types occurs also in the bobolink (*Dolichonyx oryzivorus*), and only the most common song types persist in the population from year to year (Avery and Oring, 1977). In Finland, the repertoire of song types of the same individuals of the thrush nightingale (*Luscinia luscinia*) varies from year to year. The song of a given male in a given year may become more

* Correspondence to: Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow 119234, Russia.
E-mail addresses: vladivanit@yandex.ru (V. Ivanitskii), collybita@yandex.ru (I. Marova), irishka128495@gmail.com (I. Samsonova), volodinsvoc@mail.ru (I. Volodin), volodinsvoc@gmail.com (E. Volodina).
[1] ORCID: 0000-0001-6278-0354.
[2] ORCID: 0000-0001-9755-4576.

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similar to the song of neighbors than to his own song in the previous year (Sorjonen, 1987). The average persistence of each song type of indigo bunting (*Passerina cyanea*) was estimated at 3.8 years (Payne et al., 1981, 1988). The constancy of the song types of the red-legged widow (*Vidua chalybeata*) depends on how common they are. Rare types of songs are not preserved in subsequent years. The author speculates that males may copy the types of songs of those individuals who have the greatest reproductive success. Accordingly, it may be these types of songs that persist from year to year. Nevertheless, the rate of repertoire change in the studied population was quite high. Over 8 years of observations, only half of all types of song were preserved in the population, and in a highly modified form (Payne, 1985).

In a number of other studies, the dialect features of song persisted much longer. The boundary between dialects and the structure of their constituent song types in the rufous-collared sparrow (*Zonotrichia capensis*) remained unchanged during 24 years (Kopuchian et al., 2004; García et al., 2015). The study of four populations of the white-crowned sparrow (*Zonotrichia leucophrys*) in California showed that in two large populations living in continuous, extended habitats, the song types of the local dialect have not changed over 26 years. At the same time, in populations whose habitat occupied a limited area and was largely fragmented, the structure of song types has changed significantly (Harbison et al., 1999).

Long-term preservation of a dialect was described in brown-headed cowbird (*Molothrus ater*) (O'Loghlen et al., 2013). In one of two populations studied, the constancy of song types (flight whistle song) was confirmed for a period of more than 30 years. However, in another population, this dialect has undergone rapid changes, presumably caused by the fact that the population was reduced by several harsh winters. As a result, there was a massive introduction of young dispersing individuals into the population and the "mistakes" common in the training of young individuals spread widely among the population, becoming a new "language norm" (O'Loghlen et al., 2013).

In the house finch (*Haemorhous mexicanus*), across an interval of 37 years, all the song types were completely lost and replaced by others (Ju et al., 2019). At the syllable level, half of the syllable types detected were still present decades later, although the authors argue that any two acoustic structures that are similar across time either could be homologous or could have arisen independently. The syllables that recurred in 2012 had been more prevalent in 1975, although they did not tend to maintain their prevalence in 2012 (Ju et al., 2019).

Over the course of three decades, three of the four segments of savannah sparrow (*Passerculus sandwichensis*) song showed rapid and substantive cultural evolution. Introductory sequences lost "high clusters", added "click trains" and increased the number of "clicks" in a train; middle sections shifted in their note composition and the position of the "dash note" changed; and "trills" became shorter and decreased in frequency. In contrast, the "buzz" segment remained relatively constant over the three decades of the study period (Williams et al., 2013). According to the authors' interpretation, long-term stability of the "buzz" segment may reflect a role for that segment in defining the species or dialect of the singer, just as the terminal trills of white-crowned sparrow songs remained constant within populations over 25 years while other portions of the songs changed (Nelson et al., 2004).

The chaffinch is definitely the "lab rat" of European bioacoustics. Its song has been studied in detail (Marler, 1952; Slater and Ince, 1979; Slater et al., 1980, 1984; Lynch and Baker, 1993, 1994; Böhner and Wistel-Wozniak, 1995; Lachlan and Slater, 2003; Lachlan et al., 2013; Cooper, 2020). The chaffinch is known as a closed-ended learner with a sensitive period of about 13 months (Thorpe, 1958). In particular, the chaffinch song has been the subject of two longitudinal studies. The song variation in a population of the island subspecies (*F.c. gengleri*) was investigated in England across 18 years (Ince et al., 1980). Another study was conducted in Germany in a population of the continental subspecies (*F.c. coelebs*) also across 18 years (Conrads, 1986). In this article, we analyze a time span more than twice as long. We present data on the short-term and long-term variation in the population repertoire of chaffinch songs by comparing the recordings made across intervals of 4 and 42 years (in 1978, 1982 and 2020) at the Zvenigorod biological station of Lomonosov Moscow State University (Moscow region, Russia). In addition, for estimating the spatial variability of the song, we compare the recordings made at the Zvenigorod biological station with those made of 50 km apart in the city of Moscow (in 2019).

2. Materials and methods

We analyzed our recordings of songs of unmarked male chaffinches *Fringilla coelebs coelebs* made at the Zvenigorod biological station of Lomonosov Moscow State University in 1982 (190 individuals) and 2020 (110 individuals) and the recordings made in 2019 in the city of Moscow (79 individuals). In addition, we used for comparison a catalog of song types compiled for recordings made at the Zvenigorod biological station in 1978 by G.N. Simkin. A large volume of recordings made in 1982 and 2020 was sufficient for analyzing the frequency of use of different song types. However, the number of males recorded in 1978 remained unknown, so we could not estimate the frequency of particular song types.

In 1978 and 1982, the recordings were made on analog tape recorders with a tape extension speed of 9.5 cm/s. These recordings were digitized using an IBM computer with a Creative Sound Blaster Audigy FX sound card. We used 16-bit analog-to-digital conversion of analog input at 44.1 kHz sampling rate. For sound recording in 2019 and 2020 (sampling rate 44.1 kHz, 16 bit resolution), we used the solid-state recorders Marantz PMD-660 with Sennheiser K6-ME66 cardioid electret condenser microphones. Each individual male chaffinch was recorded only once from a distance of 10–15 m. Because the chaffinches were not marked, we made special efforts to avoid re-recordings of the same male during one season. Given the large territory of the Zvenigorod biological Station and the large number of chaffinches living here, this did not pose a problem. The chaffinch is a species with a small repertoire. One male performs from one to six song types, most often only two song types (Thorpe, 1958; Kislyakov and Ivanitskii, 2018). We recorded each chaffinch until the first switch to a new song type or stopped recording after performing twenty identical songs. Therefore, the individual repertoires of a number of males were presumably not captured comprehensively.

Thus, we analyzed four samples: three from Zvenigorod (1978, 1982, 2020) and one from Moscow (2019). For each of the samples, we have compiled a catalog of song types. The song types were identified and then compared visually by their image on the spectrogram created in Syrinx 2.5s (software developed by John M. Burt; University of Washington, Department of Psychology, Seattle, WA 98195, USA) with settings FFT = 512 and Blackman window. Two observers (VI and IS) classified the song types independently and songs that were classified identically with both researchers were included in the analysis. There were no discrepancies between observers regarding the attribution of songs to types. Chaffinch songs are known to have a clear typological organization, so the identification of song types in this species is not difficult (Slater et al., 1980). In accordance with the recommendations of Mundinger (1982) and Tracy and Baker (1999), we assigned to one song type all the individual songs identical in the set of syllables and the order of their execution, as well as songs that differed by no more than 25 % of the syllable composition. The number of repetitions of the same syllables performed in a row usually varies even within one male; however, we do not consider this variability when identifying the song types. For all the song samples (apart of Zvenigorod 1978), we analyzed the proportion of males performing this song type. We used the software packages STATISTICA V. 8.0 (StatSoft Inc., USA) for statistical analysis.

3. Results

The song type catalogs of 1978 and 1982 were only slightly different.

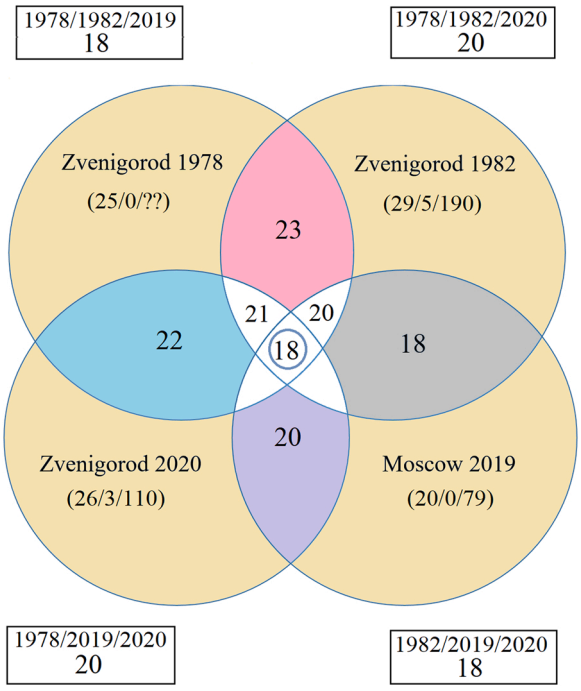

Fig. 1. The numbers of shared song types among the samples obtained from two areas and four years of recording. Each circle corresponds to one sample. The figures in parentheses show: 1) the total number of song types; 2) the number of unique song types identified in each sample; 3) the total number of males recorded. The number of song types shared between two samples is shown by the figure at the intersection of the circles. The number of song types shared between three samples is shown by the figure in rectangles. The number in the center of the figure shows the number of song types common to all four samples.

Two song types (out of 25 song types) performed in 1978 was not found in 1982, when there were six song types (out of 29 song types) which had not been performed before. There were greater differences between 1982 and 2020. In total, eight of the 29 song types (27.6 %) identified in 1982 were not found in 2020, and 5 of the 26 song types (19.2 %) discovered in 2020 were completely new compared to 1982. All the other song types recorded in 2020 were similar to the song types of 1982 at least when using the criterion of 25 % differences in syllable composition (Fig. 1).

Examples of song types of varying degree of similarity between 1978/1982 and 2020 are shown in Fig. 2. Song types A, B, C, D, E, F, and G remained largely unchanged during the observation period. Only minor variations in time and frequency parameters of some syllables have occurred. The rest of song types illustrated have changed to a greater extent up to 2020, but still have retained a clear similarity with ones recorded in 1978/1982. In the song type H, the song end flourish has changed and one syllable type present in 1978 was missing. The central phrase in the song type I changed significantly between 1978 and 2020, however, the basic structure of the composing syllables was preserved. In song type J in 2020, the first phrase was completely replaced. In song type K, the second phrase was replaced in 2020. In song types L and M in 2020, the first phrase was modified, but still clear resembled that in songs of 1978. A total of 11 song types were preserved between 1978 and 2020 almost unchanged, retaining a complete set of phrases and elements. Another four types of songs in 1978 and 2020 differed in one phrase, but had a noticeable similarity.

Thus, our data shows that the repertoire of chaffinch songs displays a substantial interannual stability for more than 40 years. Data on the performance frequency of different song types in 1982 and 2020 are presented in Fig. 3. Correlation between the two data sets is statistically significant (n = 34; Spearman rank correlation R = 0.357; P = 0.041). Hence, song types, which were more widespread in 1982, were also significantly more widespread in 2020 compared to song types, which were rarer in 1982. Another result, presented in Fig. 3D, indicates that

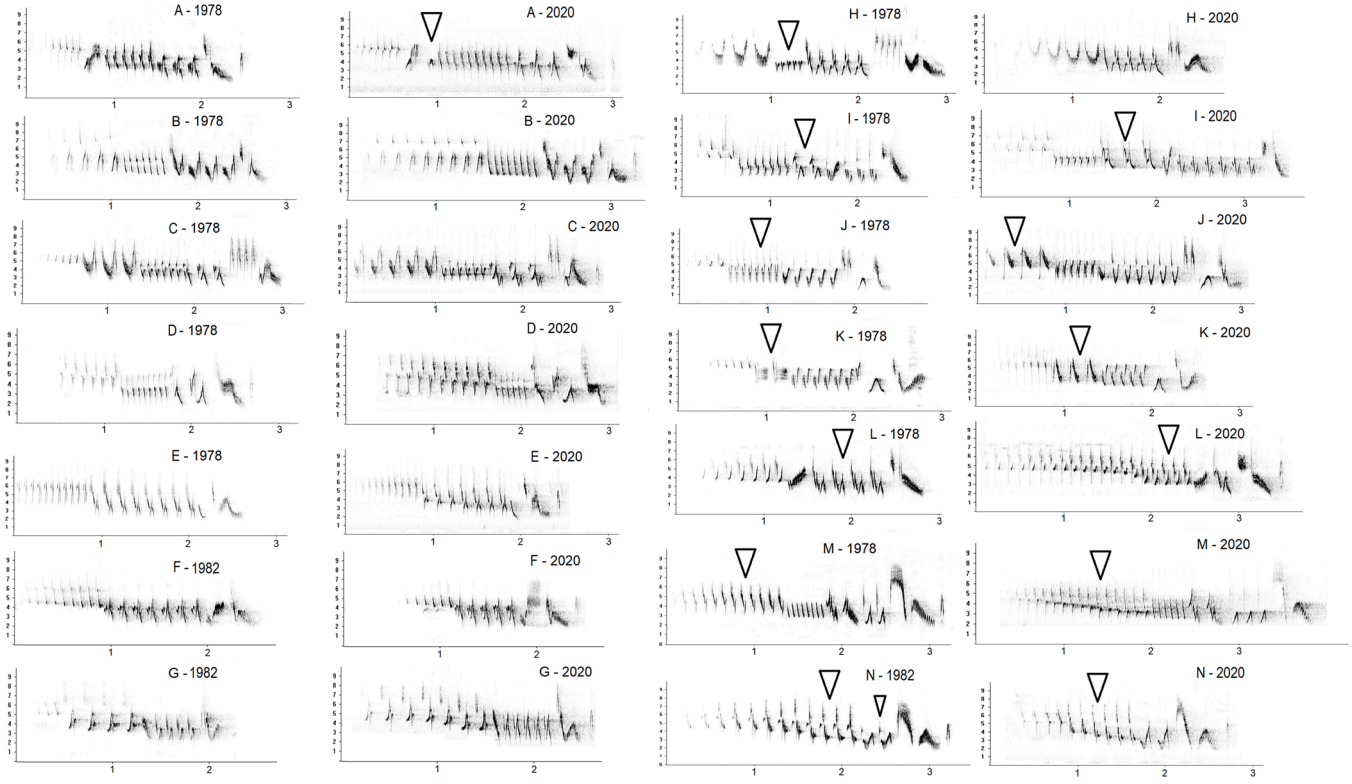

Fig. 2. Song types of male chaffinch recorded at the Zvenigorod in 1978/1982 and 2020. Similar in structure (shared) song types are marked with the same letters. Triangles show syllables that distinguish different variants of the same song type. Horizontal axis – time (s); vertical axis – frequency (kHz).

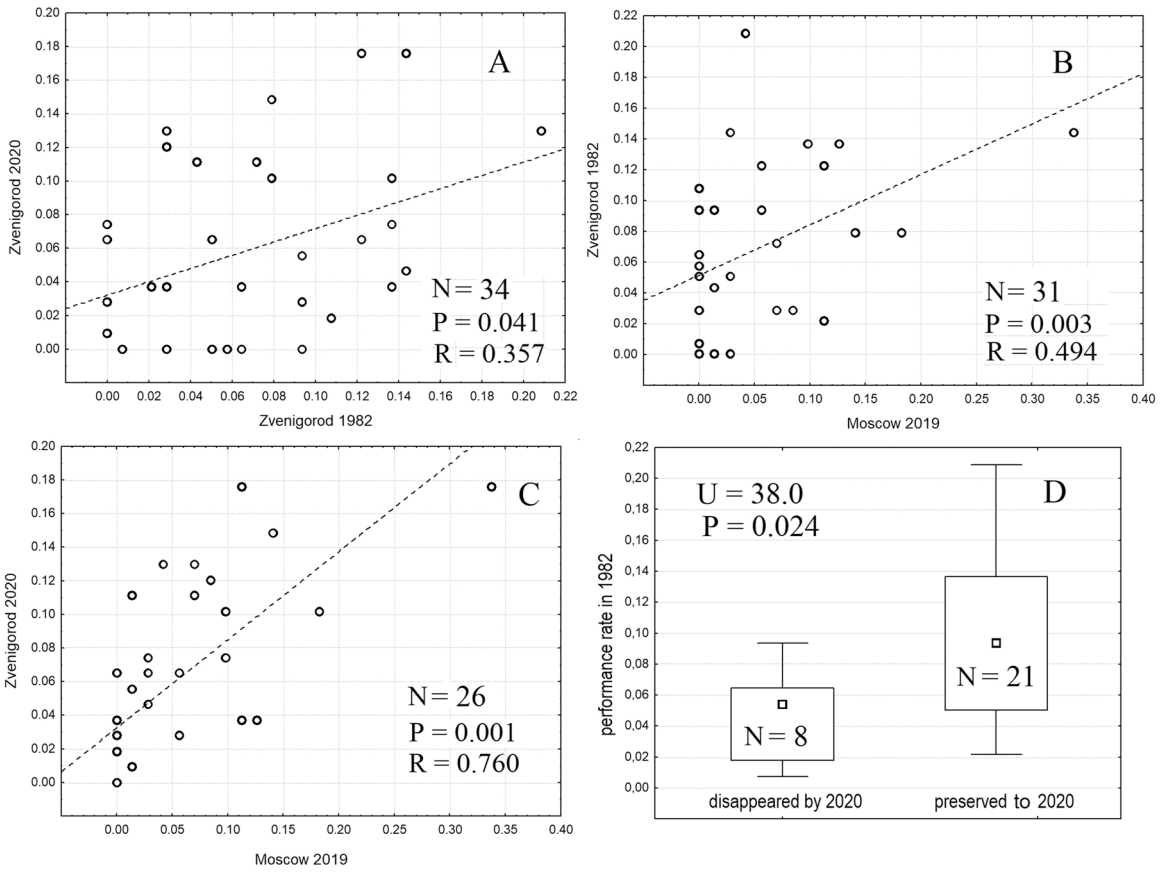

Fig. 3. The correlations between the performance rate of song types from different samples (A, B, C) and preservation over time of song types with different initial rates of performance (D; medians, quartiles, maximum and minimum values are shown). The axes show the ratio of the number of males performing this song type to the total number of recorded males. N – sample size; R – Spearman rank order correlation, U – Mann-Whitney statistics, P – statistical significance.

eight song types that disappeared between 1982 and 2020 had a significantly lower frequency of use in 1982 than the 21 song types that were still found in 2020 (P = 0.024; Mann-Whitney U Test).

A total of 20 shared song types were found between repertoires of 2019 (city of Moscow; 20 song types included) and 2020 (Zvenigorod station; 26 song types included). Only six song types found in Zvenigorod in 2020 were not found among the 20 song types of Moscow 2019 sample, whereas all these 20 song types recorded in Moscow were present in Zvenigorod 2020 sample. The correlation between the rates of use of different song types in Moscow and Zvenigorod is statistically significant (n = 26; Spearman rank order correlation R = 0.76; P = 0.001) (Fig. 3).

4. Discussion

This study showed that the repertoire of male chaffinch songs in a continental European population was remarkably stable over 4 decades. To our knowledge, such long-term stability of the population repertoire of bird song types is documented directly for the first time. Many song types remained largely unchanged over this period, while some others have changed only to a small extent, thus allowing to consider them as still the same song type. The rates of occurrence of song types were still somewhat similar between 1982 and 2020 (R = 0.357). By 2020, mainly those song types disappeared from the repertoire, which in 1982 were performed by only a few males.

Although the structural similarity of the song types performed in 1982 and in 2020 is pronounced, they might nevertheless cause different reactions from territorial males. A song type recorded today may still resemble spectrographically a song type recorded 40 years ago but the birds may not respond to it in the same way. In playback experiments conducted by Derryberry (2011), white-crowned sparrow (*Zonotrichia leucophrys*) males responded most strongly to current local songs and less to historical local songs recorded 33 years ago.

Most song types recorded at Zvenigorod biological station were also found in the city of Moscow separated by a distance of about 50 km. Some song types of male chaffinch are known to have a much wider geographic distribution, over 500 km (Simkin and Schteinbakh, 1988; Böhner and Wistel-Wozniak, 1995; Yablonovska-Grishchenko, Grishchenko, 2007; Kislyakov and Ivanitskii, 2018; Ivanitskii et al., 2021). Thus, the song types of the chaffinch show a remarkable stability over time and space. Apparently, both modes of song variability (time and space) are interrelated. The more widespread a particular song type is, the higher the chances that it will be learned by the following generations (Avery and Oring, 1977; Payne, 1985). Since the song of the chaffinch is well known to be inherited culturally, such high stability indicates the high efficiency of both horizontal and vertical cultural transfer.

As far as we know, the song of the chaffinch has been the subject of two longitudinal studies. In Germany, one song type was recorded in 1963/1964 and then in 1983/1984 in several localities dispersed over about 15 km. After 19–21 years, this song type has been preserved everywhere with minor variations (Conrads, 1986). Another study was conducted in the chaffinch population in southern England with an interval of 18 years. During this period, the number of song types in the population increased from 23 to 35. Of the 23 song types recorded in 1960, 8 song types showed clear similarity with the songs of 1978, but only 3 of them retained with minor changes (Ince et al., 1980). Thus, the survival rate of song types in England was much lower than that in Zvenigorod. This difference can be explained by the differences in the total area of study habitats and the number of chaffinches in the studied

populations. The Stanmer Great Wood (Sussex, Great Britain), where Ince and coworkers made their recordings of chaffinch songs, is a small isolated parkland with an area of only 61 ha (https://www.woodlandtrust.org.uk/visiting-woods/woods/stanmer-great-wood/). In 1978, 42 male chaffinches were recorded here and, according to these authors judgment, they recorded almost all the singing males. In contrast, Zvenigorod biological station is a part of a continuous forest area of more than 20 km^2, which is inhabited each breeding season by at least several hundred chaffinches with a high population density. Probably, the population repertoire of song types in such large population is much more stable than in small and isolated populations as e.g., island populations of chaffinch (Lachlan et al., 2013). Overall, these data suggest that change of this culturally transmitted song traits proceeds more rapidly in smaller populations occupying structurally fragmented habitats than in larger populations occupying large contiguous habitat patches (Harbison et al., 1999; Luther and Baptista, 2010; Lachlan et al., 2013).

The rate of habitat alteration can affect the site fidelity and consequently the rate of changes in vocal patterns in songbirds. Studying the song of the dickcissel (*Spiza americana*) Parker et al. (2022)found high average site fidelity in relatively stable native grasslands and much lower average site fidelity in nearby cropland sites which were disturbed by farming practices during the breeding season. They also found higher levels of average song similarity and slower average changes in vocal culture in grasslands relative to croplands. Holland et al. (1996) reported that changes in land use and suitability of habitat were responsible for the massive alteration over 18-year period in both the location and the acoustic structure of the corn bunting (*Miliaria calandra*) dialects in England. Similarly, Trainer (1983) attributed the movement of dialect boundaries in *Zonotrichia leucophrys nuttalli* to alterations in the available habitat.

The chaffinch habitats at the Zvenigorod biological station as well as in the surrounding areas of Moscow region underwent profound changes because of a bark beetle (*Ips typographus*) invasion in 2010–2014 (Komarova, 2015). Since that time, almost all the old spruce plantations have died here. By now, the overall appearance of forest vegetation has changed dramatically over a huge area in the Moscow region (Komarova, 2015). However, even such large-scale changes in habitat structure seem to be unable to change radically the population repertoire of the chaffinch songs.

The well-known great site fidelity of chaffinches in both sedentary and migratory populations may be an important reason for the high stability of their population repertoires (Mikkonen, 1983; Browne, 2004). More than 40 % of ringed adult chaffinches in the European populations return to their previous nesting site next year, and at least 30 % of first-year birds settle no further than 30 km from their birthplace next spring (Sokolov, 1991).

Many songbird species copy model songs with amazing accuracy and minimal errors during vocal training. As a statistical estimate of cultural change over time shows, theoretically, this may entail the preservation of vocal traditions in songbirds for many hundreds of years, which is quite comparable to the duration of the existence of traditions in human society (Lachlan et al., 2018). The study we have done confirms more than forty years of stability of the population repertoire of the chaffinch and seems to indicate such a possibility.

Declaration of Competing Interest

The authors declare that there are no conflicts of interest.

Data Availability

Data will be made available on request.

Acknowledgements

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