

Geographic variations of song and rain calls of the Chaffinch across the ranges of three subspecies

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Abstract We analyze the variability of the Chaffinch’s (*Fringilla coelebs*) song and rain calls in 20 populations localized along a transect of about 3,000 km, crossing the territory of European Russia between the White Sea, Crimean Peninsula and the Caucasus Mountains. Three subspecies of Chaffinch inhabit this area: European (*F. c. coelebs*), Caucasian (*F. c. caucasicus*), and Crimean (*F. c. solomkoi*). The results of cluster analysis based on song show that the populations of Crimea and southeastern Dagestan stand out the most. All other populations fall clearly into two clusters corresponding to the European and Caucasian subspecies. In most of the European subspecies vast range in Russia, the “buzzing” dialect of the rain call is widespread. Only in the extreme north-west of Russia, it is replaced by a whistling dialect. In most of the Caucasus and in the Ciscaucasia, Chaffinches also emit exclusively whistling sounds, but of a completely different structure. In the Western Caucasus, Chaffinches perform also a whistling call having a unique two-syllable structure. The Crimean peninsula is inhabited by whistling Chaffinches as well, although the frequency modulation of its call is different from that of Caucasian subspecies. We discuss the spatial distribution of song types and of rain calls dialects within the ranges of subspecies and in the contact zones between them.

Keywords: vocal dialects, population bioacoustics, contact zones, *Fringilla coelebs*

Összefoglalás Az erdei pinty énekének és esőhívó hangjának variabilitását elemeztük 20 populációban, melyek egy 3000 km-es transzekt mentén találhatóak, átszelve Oroszország európai részét a Fehér-tenger, a Krím-félsziget és a Kaukázus között. Az erdei pinty (*Fringilla coelebs*) három alfaja él ezen a területen: az európai (*F. c. coelebs*), a kaukázusi (*F. c. caucasicus*) és a krími (*F. c. solomkoi*). Az éneken alapuló klaszteranalízis eredményei azt mutatják, hogy a krími és a délkelet-dagesztáni populációk térnek el leginkább. Az összes többi populáció egyértelműen két különböző klaszterbe esik, amelyek az európai és kaukázusi alfajoknak felelnek meg. Az európai alfaj hatalmas oroszországi elterjedési területének nagy részén az esőhívó hang „zümögő” dialektusa jellemző. Csak Oroszország legészaknyugati részén váltja fel a füttyülő dialektus. A Kaukázus és Ciszkaukázus nagy részén az erdei pintyek kizárólag füttyülő hangokat is kiadnak, de ezek teljesen más szerkezetűek. A Nyugat-Kaukázusban az erdei pintyek egyedi, kétszillabusos szerkezetű füttyülő hangot is használnak. A Krím-félszigeten füttyülő erdei pintyek is énekel, bár ezek hangjainak frekvencia modulációja különbözik a kaukázusi alfajétól. Az énektípusok és az esőhívó hang dialektusainak térbeli eloszlását az alfajok elterjedési területén belül és a közöttük lévő kontaktzónában tárgyaljuk.

Kulcsszavak: ének dialektusok, populáció bioakusztika, érintkezési zónák, erdei pinty

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Introduction

For many years, ornithologists and bioacousticians have been fascinated by geographical variations in songbirds singing. Many reasons contribute to the interest in this subject, including the problems of speciation and taxonomy (Payne 1986, Alström & Ranft 2003). Song is known as a key factor in reproductive isolation between closely related songbird species under sympatric conditions (Qvarnström *et al.* 2006, Kenyon *et al.* 2017). The song of songbirds has an innate basis, however, for its full development a young bird must hear and remember the singing of adults of its species. Therefore, the structural features of the song are independently transmitted from generation to generation, both through genetic inheritance and through vocal learning (Catchpole & Slater 2008). This results in a complex spatial variation of the song, which is studied at different levels: from local populations to the whole range of the species or a significant part of it (Mundinger 1982, Martens 1996, Podos & Warren 2007, Pitocchelli 2011, Petrusková *et al.* 2015, Kaluthota *et al.* 2016).

The Chaffinch (*Fringilla coelebs*) inhabits a huge range stretching from the British Isles and North Africa to the Baikal Lake in Central Siberia. The geographical variability of the Chaffinch's song has been known for a long time (Promptov 1930, Marler 1952) and has attracted much attention from researchers (Slater *et al.* 1980, Conrads 1986, Lynch & Baker 1993, 1994, Lachlan & Slater 2003). Nevertheless, the number of studies analyzing the variability of the song of this species in an area comparable to the size of its range remains limited (Slater *et al.* 1984, Böhner & Westel-Wozniak 1995, Yablonovka-Grishchenko & Grishchenko 2007, Astakhova 2012).

In this article, we analyze the variability of the Chaffinch song along a transect of about 3,000 km, crossing from north to south the territory of European Russia between the White Sea, Crimean Peninsula and the Caucasus Mountains. Three subspecies of Chaffinch inhabit this vast area: European (*F. c. coelebs*), Caucasian (*F. c. caucasicus*), and Crimean (*F. c. solomkoi*). We consider the variations of the song within the ranges of these subspecies and focus in more detail on the patterns occurring on the borders between them.

The rain call is a special acoustic signal of the Chaffinch, which is often emitted by males during the breeding season. Along with the song, the rain call is the subject of close attention of researchers. Several dialects of rain call have been described in Central and Eastern Europe. Some dialects occupy a limited area; others have a very wide distribution (Baptista 1975, Bergmann 1993, Sorjonen 2001, Ivanitskii *et al.* 2021). All the subspecies studied by us have clearly distinct rain call dialects, and the European and Caucasian Chaffinch has two dialects, so we also consider the degree of correspondence between spatial variability of the population repertoires of song types and rain calls.

Materials and Methods

From 2017 to 2022, we recorded 1,061 Chaffinches in 20 populations representing three subspecies. The distance between the northernmost (White Sea) and the southernmost (Dagestan) recording points is about 3,000 km. Our recordings were made on a Marantz

Table 1. The recording areas, number of male recorded, song types, and endemic song types found

1. táblázat A mintavételi területek, a hímek, a daltípusok és az endemikus daltípusok száma

	recording areas	coordinates	number of males recorded	number of song types found	number of endemic song types
1	the city of Kandalaksha (White Sea)	67°09'N 32°25'E	48	23	5
2	Belomorskaya Biological Station (White Sea)	66°32'N 33°06'E	18	16	0
3	Pinezhsky Nature Reserve (Arkhangelsk Region)	64°54'N 42°41'E	44	19	1
4	the city of Sortavala (Karelia)	61°42'N 30°42'E	130	31	1
5	Piysieki village (Karelia)	62°01'N 32°06'E	71	29	0
6	Pryazha village (Karelia)	61°41'N 33°36'E	38	26	0
7	Darwinsky Nature Reserve (Rybinsk Reservoir)	58°43'N 37°47'E	99	29	2
8	Zvenigorodskaya Biological Station	55°42'N 36°45'E	112	27	1
9	the city of Moscow	55°43'N 37°35'E	71	20	1
10	Gornensky Forestry (Rostov region)	47°50'N 40°14'E	35	11	6
11	the city of Rostov-on-Don	47°15'N 39°43'E	37	27	6
12	Alexandrovsky forestry (Rostov region)	46°44'N 39°07'E	41	22	5
13	Novopokrovskaya village (Krasnodar Region)	45°56'N 40°41'E	46	18	1
14	Western Kalmykia	46°04'N 41°55'E	27	17	3
15	Crimean Peninsula	44°48'N 34°32'E	90	34	26
16	Utrish village (Abrau Peninsula, Black Sea coast)	44°45'N 37°23'E	31	34	3
17	Djanhot village (Black Sea coast)	44°46'N 38°16'E	25	27	3
18	the city of Kislovodsk (Ciscaucasia)	43°53'N 42°43'E	25	13	0
19	Dombai village (Northern Caucasus)	43°16'N 41°37'E	23	19	3
20	Samursky National Park (Dagestan)	41°51'N 48°30'E	50	28	28

PMD 660 digital audio recorder with a Sennheiser ME 66 condenser microphone equipped with a K6 preamplifier. The list of location studied, their geographic coordinates, the number of males recorded, the number of song types and the number of endemic song types found in each location are presented in *Table 1*. The positions of all the locations on the geographical map are shown in *Figure 1*.

The vocal session of the Chaffinch consists of distinct songs separated by clear pauses. Each individual song belongs to a certain type (i.e. a stereotypical acoustic construction that is repeated many times in the singing of a given male, in the singing of several males from a given population or even from other populations) (Slater *et al.* 1980, Conrads 1986). We identify song types by visual inspection of sonograms. We consider different renditions of song as belonging to the same song type if they have the same set of syllable



Figure 1. The recording points: 1 – the city of Kandalaksha; 2 – Belomorskaya Biological Station; 3 – Pinezhsky Nature Reserve; 4 – the city of Sortavala (Karelia); 5 – Piysieki village (Karelia); 6 – Pryazha village (Karelia); 7 – Darwinsky Nature Reserve; 8 – Zvenigorodskaya Biological Station; 9 – the city of Moscow; 10 – Gornensky forestry (Rostov region); 11 – the city of Rostov-on-Don; 12 – Alexandrovsky forestry (Rostov region); 13 – Novopokrovskaya village (Krasnodar Region); 14 – Western Kalmykia; 15 – Crimean Peninsula; 16 – Utrish (Abrau Peninsula); 17 – Dzhanxhot village; 18 – the city of Kislovodsk; 19 – Dombai village; 20 – Samursky National Park (Dagestan). The sharp angle of the black triangle identifies the exact location of the recording point

1. ábra A mintavételi pontok: 1 – Kandalaksha városa; 2 – Belomorskaya Biológiai Állomás; 3 – Pinezhsky Természetvédelmi Terület; 4 – Sortavala városa (Karélia); 5 – Piysieki falu (Karélia); 6 – Pryazha falu (Karélia); 7 – Darwinsky Természetvédelmi Terület; 8 – Zvenigorodskaya Biológiai Állomás; 9 – Moszkva városa; 10 – Gornensky erdészet (Rosztov régió); 11 – Rostov-on-Don városa; 12 – Alexandrovsky erdészet (Rosztov régió); 13 – Novopokrovskaya falu (Krasnodar régió); 14 – Nyugat-Kalmykia; 15 – Krím-félsziget; 16 – Utrish (Abrau-félsziget); 17 – Dzhanxhot falu; 18 – Kislovodsk városa; 19 – Dombai falu; 20 Samursky Nemzeti Park (Dagesztán). A fekete háromszögek hegyes szöge jelöli a felvételi pontok pontos helyét

types performed in the same sequence. Two obviously similar songs were assigned to the same type, even if they differed in one type of syllable. Songs ending with different flourish have always been classified as different types. The number of repetitions of the same syllables performed in a row within a song usually varies even in one male; however, we do not consider this variability when determining song types. The song types in the Chaffinch are strictly stereotyped and reliably differ from each other, therefore, their identification on the sonogram usually does not constitute a problem. The individual repertoire of a male Chaffinch includes from one to six (usually 2–3) song types; in a local and fairly large settlement of Chaffinches, usually several dozen song types could be recorded (Slater *et al.* 1980).

The spectrograms were 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. We used the software packages STATISTICA V. 8.0 (StatSoft, Inc.USA) and PAST V. 2.13 (Hammer *et al.* 2001) for statistical data processing. For each population, we calculated the variety of song types and the number of males performing them (in percentage of the total number of males studied in this population). We used cluster analysis with the unweighted pair-group average as combining algorithm and the Jacquard coefficient (for a variety of song types) and the Bray-Curtiss metrics (for the number of performing males) as a similarity measure.

Results

A total of 179 song types have been identified in 20 populations. The number of song types found in one population varied from 11 to 34, with an average of 23.5 ± 6.7 . More than half of the song types (54.2%) were performed in one population, while 38 song types were recorded in five or more populations, and one song type was found in 10 populations, localized across a space of more than 2,000 km from Kandalaksha to Rostov-on-Don (*Figure 2*).

The results of cluster analysis are presented in *Figure 3*. Two different clustering methods revealed a very similar pattern. The results of the analysis of the simple similarity of population repertoires and numerical ratios of males performing different song types show only few differences. Among all the populations studied, the Crimean and Dagestan populations stand out the most. In Crimea, we identified 34 song types, of which eight song types were found in the nearest population of Utrish (Abrau Peninsula) and five from the latter were identified in the Dzhanhot population localized 60 km to the south-west from the Utrish. All the other 26 Crimean song types were endemic.

The population from southeastern Dagestan is largely removed from other populations of the Caucasian subspecies studied. This can be explained by that the Samursky National Park is a rather isolated forest area, bounded from the east by the Caspian Sea and from the north, west and south it is surrounded by arid mountains, steppe areas and cultivated lands. All 28 song types recorded in Dagestan turned out to be endemic and were not found in any of the populations from the Caucasus or from the Ciscaucasia. In particular, no shared song types were found with the nearest populations of Kislovodsk and Dombai, located 580 km from

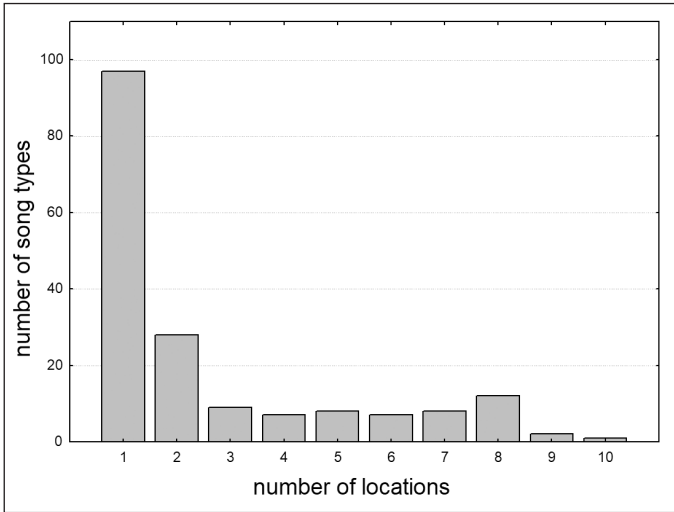


Figure 2. Frequency of the song types performance. The horizontal axis is the number of localities in which song types were performed; the vertical axis is the number of song types.

2. ábra Az énektípusok gyakorisága. A vízszintes tengely mutatja a helyszínek számát, ahol az énektípusokat énekeltek; a függőleges tengely mutatja az énektípusok számát

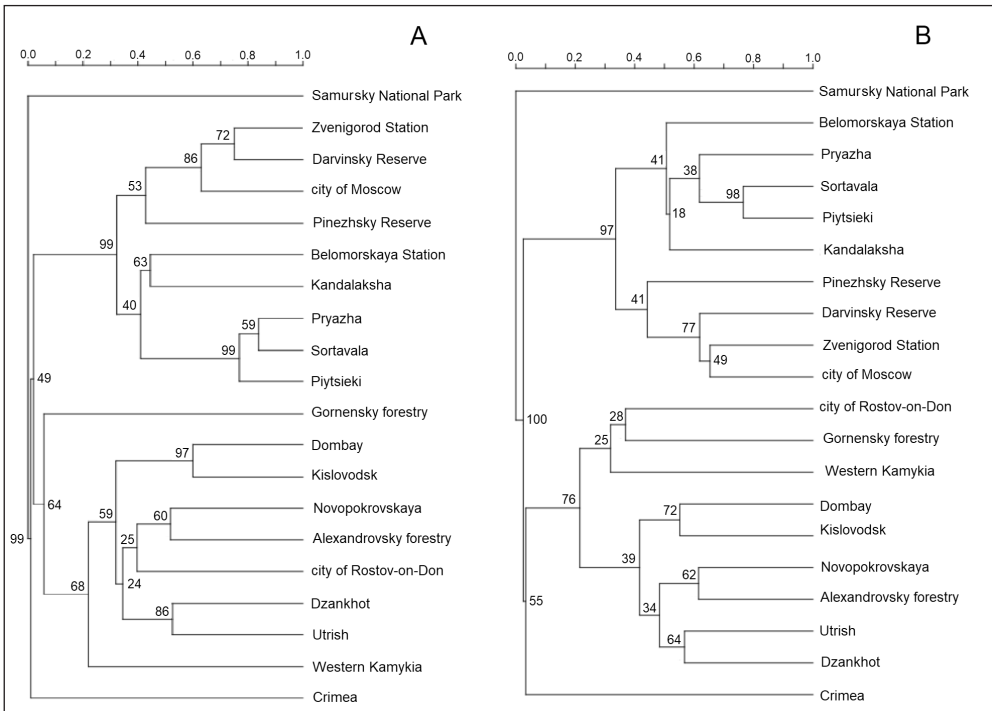


Figure 3. Similarity of the song types repertoires of the 20 populations studied. A – according to the presence/absence of song types in the repertoire of the population; B – according to the number of males performing this song type (in percentage of the total number of male recorded in the population)

3. ábra Az énektípus repertoárok hasonlósága a 20 vizsgált populációban. A – az énektípus a populáció repertoárjában való jelenlétének/hiányának megfelelően; B – az énektípust előadó hímek számának megfelelően (a populációban felvett hímek teljes számának százalékában)

the Samursky forest while 10 shared song types were found between Dombay and Rostov-on-Don, separated by comparable distance 480 km.

All other populations studied fall clearly into two large clusters corresponding to the European and Caucasian subspecies. Three clusters with good bootstrap support are distinguished within the European subspecies. One of them unites three populations found relatively close to each other: the city of Moscow, Zvenigorodskaya station, and the Darwinsky Reserve located about 270 km from Moscow. In another cluster, three points in Karelia are united with almost absolute bootstrap support. The distance between them is about 90–150 km. Kandalaksha and Belomorskaya stations are connected to the third cluster, but with less support. These populations are separated from Karelia by a distance about 600 km, and they are about 65 km from each other. Finally, the population of the Pinezhsky Reserve occupies a separate position in the cluster of the European subspecies. It is separated from the nearest White Sea population by a distance of 450 km.

There are also three groups with good bootstrap support within the Caucasian cluster (*Figure 3*). The first one combines the populations of Dombay and Kislovodsk, located 100 km from each other, with 12 shared song types. Second cluster includes population of the Utrish and Dzhanhot with 21 shared song types and the distance between them 60 km. The third cluster unites the Chaffinch populations of the Alexandrovsky Forestry and Novopokrovskaya, localized 150 km from each other with 14 shared song types.

Exactly the same distance of 150 km separates Gornensky and Alexandrovsky forestry, but only two shared song types were found between them. These two forestries are inhabited by different subspecies (the European subspecies in the Gornensky forestry and the Caucasian subspecies in the Alexandrovsky forestry). The city of Rostov-on-Don is located just in the middle between these two forestry and it has 14 song types shared with the Alexandrovsky forestry and six song types shared with the Gornensky forestry. For comparison, the cities of Rostov-on-Don and Dombay are located 500 km from each other and have 10 shared song types. Thus, the population of Rostov-on-Don, from the point of view of the song type distribution, tends more to Caucasian subspecies.

It is important to note that many song types of the Chaffinch are present unchanged even in populations that are very remote from each other. For example, in the population repertoires of the city of Moscow and the Darwin Reserve, separated by 280 km, 19 shared song types were found; in the repertoire of Moscow and the Pinezhsky Reserve, the distance between which is 1,100 km, nine shared song types were identified. Even in the populations of Moscow and Kandalaksha, separated by a distance of 1,300 km, seven shared song types were found. A similar situation occurs within the Caucasian subspecies. For example, 11 shared song types were found between Novopokrovskaya and Dombay. These two points are 300 km away from each other, and Chaffinches live here in completely different conditions: in the broad-leaves forests on the plain of the Ciscaucasia (Novopokrovskaya) and in mountain coniferous forests at an altitude of 1,600 m above sea level (Dombay).

Let us now consider the relationship between the distribution of song types and the rain calls of Chaffinch. In most of the European subspecies vast range in Russia, the “buzzing” (“wrüt”) dialect of the rain call is widespread (*Figure 4A*). Only in the extreme north-west of Russia (in Karelia), it is replaced by a whistling dialect (*Figure 4B*). In most of the Caucasus

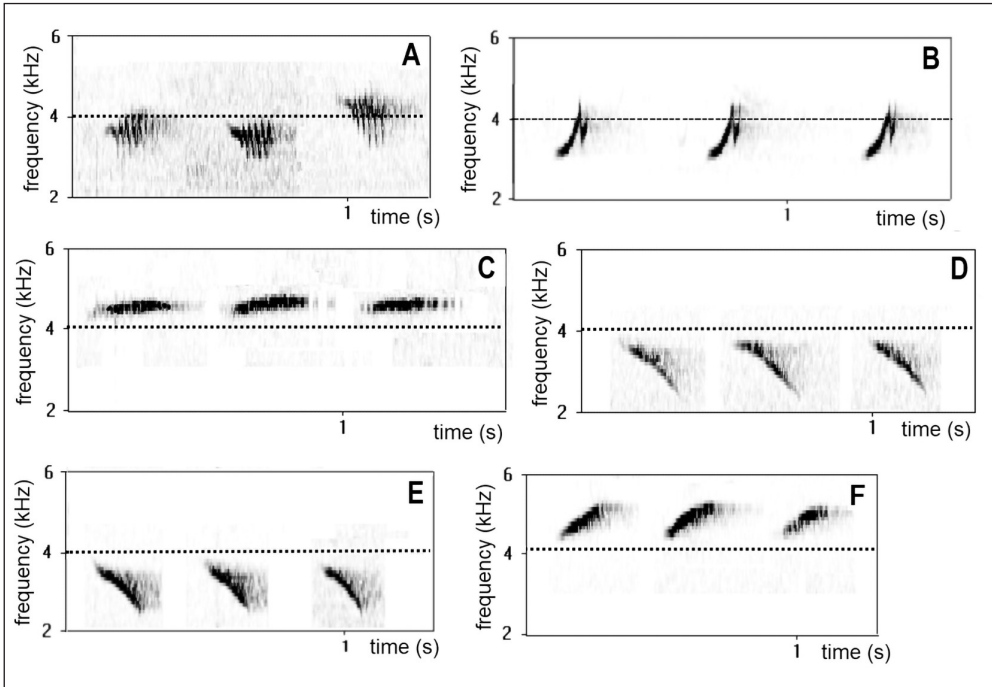


Figure 4. Example sonograms of rain calls: A – buzzing (“wrüt”) dialect; B – north-western (“hüid”) dialect; C – Crimean dialect; D – central and eastern Caucasus dialect; E and F – western Caucasus dialect

4. ábra Példák esőhívó hangok szonogramjára: A – zümmögő („wrüt”) dialektus; B – északnyugati („hüid”) dialektus; C – krími dialektus; D – közép- és kelet-kaukázusi dialektus; E és F – nyugat-kaukázusi dialektus

and in the Ciscaucasia, Chaffinches also emit exclusively whistling calls; however, the structure of the latter is sharply different from that of the northern one (Figure 4C). In the Western Caucasus, Chaffinches perform also a whistling call having a unique two-syllable structure (Figure 4E, F). Finally, the Crimean peninsula is inhabited by whistling chaffinch as well, although the frequency modulation of its call (Figure 4D) is quite different from that of Caucasian subspecies (Ivanitskii *et al.* 2021).

According to our observation, in Kandalaksha and at the Belomorskaya station all the chaffinches whistle while in the Pryazha they buzz. Sortavala and Piytsieki are located in the mixing zone of these call dialects. The Chaffinches found here use both buzzing and whistling calls, as well as a variety of intermediates between them. Thus, the border between the dialects of the rain calls in Karelia is expressed quite clearly, which cannot be said about the song types distribution. Between Pryazha and Kandalaksha, belonging to different rain call dialects and located 600 km from each other, 12 shared song types were found, which is about half of their population repertoires.

The situation looks different in the contact zone of the European and Caucasian subspecies in the Rostov-on-Don region. The population of Rostov-on-Don looks transitional between the European and Caucasian subspecies, which is also confirmed by the distribution of rain

call types in this region. According to our observations, both buzzing (European subspecies) and whistling (Caucasian subspecies) Chaffinches are found in the city in approximately equal proportions. Thus, there is a clear boundary here between both the population repertoires of song types and the dialects of the rain call.

The Kerch Strait clearly separates the Crimean and West Caucasian dialects of rain calls. In Crimea (including Feodosia and Koktebel as an easternmost recording points), Chaffinches emit monosyllabic repetitive whistling signals with descending frequency modulation. In the western Caucasus (including Utrish and Dzhanikhot as a westernmost recording points), the rain calls have a two-syllable structure and sound like a fairly regular alternation of whistling signals with descending and ascending modulation. Finally, throughout the rest of Caucasus (to the east of the Sochi), as well as throughout the Ciscaucasia, Chaffinches emit a typically “Caucasian” dialect: monosyllabic whistling signals with flat or slightly increasing frequency modulation (Tsvelykh & Yablonovska-Grishchenko 2012, Ivanitskii *et al.* 2021).

Discussion

All researchers who studied the distribution of Chaffinch song types over large areas pay attention to the similarity of repertoires even in the most remote populations (Slater *et al.* 1984, Simkin & Steinbach 1988, Yablonovska-Grishchenko & Grishchenko 2007, Astakhova 2012). Our results also reveal an extremely wide distribution of many song types within the ranges of the European and Caucasian subspecies (*Figure 5*).

Thus, in the Chaffinch, cultural continuity ensures the transfer of vocal models (song types) over a distance of 1,300 km. It is not known, however, how long does it take for the song types to spread over such a distance. For example, the spread of a new variant of the White-throated Sparrow (*Zonotrichia albicollis*) song from west to east across Canada was observed; this variant replaced the existing song over approximately four decades (Otter *et al.* 2020). Obviously, it is necessary for this that the song types, spreading to new areas, would remain unchanged in the original area of their distribution. The song types are known to persist in populations of some species for decades (Harbison *et al.* 1999, Goodale & Podos 2010, O’Loughlen *et al.* 2013, García *et al.* 2015, Jäckel *et al.* 2022). We have described the survival of many of the Chaffinch song types for 38 years (from 1982 to 2020) in the population of the Zvenigorodskaya Station (Ivanitskii *et al.* 2023). It is quite possible that such a high temporal stability is one of the important prerequisites for the widespread distribution of song types in this species of songbirds.

Thus, although the number of shared song types found between any two localities undoubtedly decreases with increasing distance between the latter, many of Chaffinch song types are distributed almost throughout the range of the European and Caucasian subspecies at least within the borders of the Russian Federation. Our conclusion about the song type’s spatial consistency within the subspecies ranges and the sharp change when crossing the boundaries between them is supported by the data of Astakhova (2012). Of the 15 Chaffinch song types recorded by her in Moscow, 12 were found on the Curonian Spit of the Baltic Sea about 1,100 km from Moscow, while of the 16 song types recorded in Crimea – about

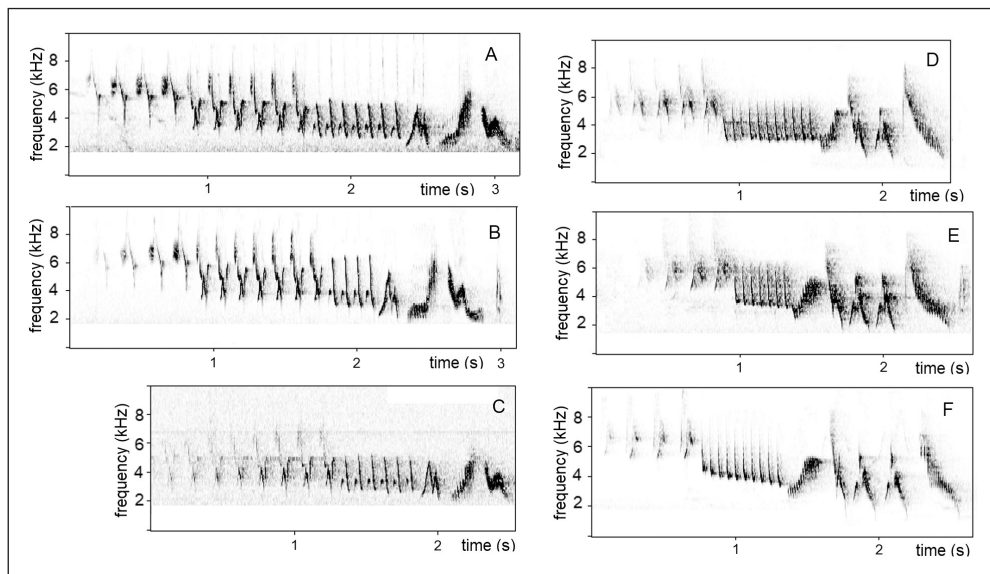


Figure 5. Example sonograms of European (A, B, C) and Caucasian (D, F) song types with a broad geographical distribution: A – Kandalaksha; B – the city of Sortavala (Karelia); C – Pinezhsky Nature Reserve; D – Alexandrovsky forestry (Rostov region); E – Western Kalmykia; F – the city of Kislovodsk

5. ábra Példák a széles elterjedésű európai (A, B, C) és kaukázusi (D, F) énektípusok szonogramjára: A Kandalaksha városa; B – Sortavala városa (Karélia); C – Pinezhsky Természetvédelmi Terület; D – Alexandrovsky erdőszet (Rosztov régió); E – Nyugat-Kalmykia; F – Kislovodsk városa

the same distance from Moscow – only one song type was found to be shared with Moscow population.

The distances to which the rain calls spread over are also very large. For example, the Caucasian dialect occupies almost the entire Ciscaucasia and the entire Caucasus (with the exception of its western part). The distance of distribution of this dialect from west to east is about 700 km. The Caucasian and Crimean subspecies are separated by the narrow Kerch Strait (from 4.5 to 15 km wide), which does not look an important obstacle to the spread of song types and rain calls. As a result, the rain call of Chaffinches in the Western Caucasus looks like a very orderly alternation of Crimean and Caucasian calls. Thus, on the border between the Caucasian and Crimean subspecies, there is an active unilateral penetration of Crimean vocal models (both song types and rain calls) to the east of the Kerch Strait, while there is no reverse movement.

As for the buzzing (“wrüt”) rain call dialect, it is the only dialect in most of the vast area inhabited by the European subspecies from north-western Germany (Bergmann 1993) to Krasnoyarsk (Ivanitskii *et al.* 2021) at a distance of over 5,000 km. The exact mechanisms that allow song types and rain calls to move hundreds and thousands of kilometers remain unknown and need further research. It is possible that the continuous distribution of the Chaffinch and its high abundance almost everywhere throughout the range (Payevsky 2020) largely contributes to the transmission of vocal models over long distances.

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