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ORIGINAL ARTICLE

Contrasting patterns of geographical song variation in two closely related passerine species with a simple song

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Abstract

Decades of research on geographic variation of birdsong have provided evidence that passerine vocalization often diverges among populations. We asked whether even songs so simple that they superficially resemble stridulating insects vary geographically. We focused on two closely related species of the genus *Locustella*, the River Warbler (*L. fluviatilis*) and the Grasshopper Warbler (*L. naevia*). At four Central European localities separated by 85–380 km, we recorded 62 River Warbler males, and at three of these sites, we also recorded 32 coexisting Grasshopper Warbler males. We hypothesized to observe differences among geographically distant populations in both species. However, only the song of River Warbler diverged among the localities in structural and quantitative parameters, especially in the number, frequency and position of high-amplitude notes within the repeated syllables. Discriminant analysis successfully classified 80% of all River Warbler males to their respective population, in agreement with our subjective classification of songs into several categories. In contrast, the populations of Grasshopper Warbler at the same spatial scale could not be differentiated either by visual inspection or by any of the measured song characteristics. Further comparison with spectrograms available from the European range of both species supported these patterns also on a larger geographical scale, with additional distinct River Warbler song types observed out of our study region, but similarly looking Grasshopper Warbler song types distributed across the continent. Different patterns of song geographic variation in the two coexisting, closely related species highlight species-specific traits that contribute to song divergence and imply the great diversity in singing behaviour among songbirds.

Keywords *Locustella* · Vocalization · Congeneric species · Simple song · Geographic variation

Zusammenfassung

Unterschiedliche Muster geografischer Gesangsvariation bei zwei nahe verwandten Singvogelarten mit schlichtem Gesang

Jahrzehntelange Erforschung der geografischen Variation von Vogelgesängen lieferte Belege dafür, dass sich die Lautäußerungen von Singvögeln oft zwischen Populationen unterscheiden. Wir stellten uns die Frage, ob sogar solche Gesänge geografisch variieren, die so schlicht sind, dass sie oberflächlich an stridulierende Insekten erinnern. Wir konzentrierten uns auf zwei nahe verwandte Arten der Gattung *Locustella*, den Schlagschwirl *L. fluviatilis* und den Feldschwirl *L. naevia*. An vier 85 bis 380 km voneinander entfernten Orten in Mitteleuropa nahmen wir 62 Schlagschwirlmännchen auf; an dreien dieser Orte machten wir außerdem Aufnahmen von 32 ebenfalls dort lebenden Feldschwirlmännchen. Wir postulierten das

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Auftreten von Unterschieden zwischen geografisch getrennten Populationen bei beiden Arten. Allerdings unterschieden sich nur die Gesänge des Schlagschwirls zwischen den Orten bezüglich ihrer strukturellen und quantitativen Parameter, hier besonders in Anzahl, Frequenz und Anordnung der Töne mit hoher Amplitude innerhalb der wiederholten Silben. Mittels Diskriminanzanalysen konnten erfolgreich 80% aller Schlagschwirlmännchen ihrer jeweiligen Population zugeordnet werden, was mit unserer subjektiven Einteilung der Gesänge in verschiedene Kategorien übereinstimmte. Im Gegensatz dazu gelang es weder durch visuelle Betrachtung noch mittels eines der erfassten Gesangsmerkmale, die Feldschwirlpopulationen im selben räumlichen Maßstab zu unterscheiden. Weitergehende Vergleiche mit für die europäischen Verbreitungsgebiete beider Arten verfügbaren Sonagramme bestätigten diese Muster auch für einen größeren geografischen Maßstab, das heißt außerhalb unseres Untersuchungsgebietes gab es beim Schlagschwirl weitere eindeutige Gesangsvarianten, wohingegen Feldschwirle kontinentweit ähnliche Gesangstypen zeigten. Das Auftreten verschiedener Muster der geografischen Gesangsvariation bei zwei gemeinsam vorkommenden, nahe verwandten Vogelarten unterstreicht artspezifische Merkmale, die zur Gesangsvielfalt beitragen und ist ein Zeichen der großen Diversität des Gesangsverhaltens bei Singvögeln.

Introduction

Geographic variation of bird song has been in focus of research for decades (Marler and Tamura 1962; Baker and Cunningham 1985; MacDougall-Shackleton and MacDougall-Shackleton 2001; Branch and Pravosudov 2020) as it might be a powerful tool for studying various aspects of bird ecology and evolution (e.g., Edwards et al. 2005; Laiolo and Tella 2005; Ryan 2006; Freeman and Montgomery 2017).

Geographic variation of vocal signals has been demonstrated in various bird species, regardless of whether their vocalisation is innate (e.g., Mager III et al. 2007; Ippi et al. 2011; Budka et al. 2014) or transmitted culturally through social learning. The latter mechanism is relevant for parrots (Wright 1996), hummingbirds (González and Ornelas 2014) and especially for songbirds (oscine passerines), which are in focus of most studies (reviewed in Podos and Warren 2007). It is apparently a general phenomenon that, as other phenotypic traits, evolves through dynamic interplay of evolutionary and ecological factors such as natural selection, sexual selection and genetic drift (reviewed in Podos and Warren 2007), modulated by individual dispersal and population connectivity (e.g., Gammon et al. 2005; Nunn et al. 2009; Fayet et al. 2014). Moreover, social interactions (e.g., Ellers and Slabbekoorn 2003; Budka et al. 2014), local adaptations of song to habitat structure (e.g., Patten et al. 2004; Van Dongen and Mulder 2006) or ambient noise (e.g., Dingle et al. 2008; Ríos-Chelén et al. 2012) may also affect song variation.

In song-learning species, however, the evolution of song divergence may be driven by additional factors, as learning may be a major source of song variation (e.g., Slater 1989; Lahti et al. 2011). Such variation of song might be further affected by cultural selection, as signals which are more effective in communication are more likely to be transmitted, and therefore, to survive longer (Lachlan et al. 2018), as well as by cultural drift, where cultural traits may be randomly fixed or lost (Podos and Warren 2007).

Given the diversity of factors that may contribute to song variation, it is not surprising that the extent of vocal divergence is highly variable among species and can be represented by the whole range of patterns—from sharing of complete song types among neighbours to no sharing at all between birds from the same location (Handley and Nelson 2005). If song characteristics change abruptly over short distances and local song variants are separated by clear borders, they are referred to as dialects (Mundinger 1982). These were documented in species with relatively simple songs (e.g., Rotstein and Fleischer 1987; Petrusková et al. 2015) as well as more complex ones (e.g., Marler and Tamura 1962; McGregor 1980). More usually, vocalization characteristics change gradually across the breeding range. Such clinal variation was described for species with different song complexity (e.g., Irwin 2000; Ramsay and Otter 2015; Sung and Handford 2006).

Nevertheless, no geographic variation of song attributable to among-population or regional differences was detected in some passerine species. This might be due to song uniformity throughout the breeding range, with songs of the same characteristics recurring frequently in distant populations, as described for passerines with simple vocalization (Bryan et al. 1987; Kroodsma et al. 1999a). Lack of clear geographic patterns may also result from extensive individual variation when each male has unique vocalization, either rich repertoire of many song types (Kroodsma et al. 1999b) or single individually specific song types (e.g., Tsipoura and Morton 1988; Janes and Ryker 2016).

The simpler the species' song is, the fewer characteristics (frequency, temporal or structural) there are to vary. In this study, we focused on potential song geographic variation of two often coexisting passerine species (Cramp 1992; del Hoyo et al. 2006), Grasshopper Warbler (*Locustella naevia*) and River Warbler (*L. fluviatilis*), from the clade of the genus *Locustella* with a particularly simple vocalization (Alström et al. 2018). Males of both species typically sing a single song type (Cramp 1992), usually consisting of repetition of only one syllable (Brackenbury 1978; Cramp 1992). Our main question was: is the song of Grasshopper Warbler and River Warbler geographically variable despite being so simple? Considering that the song of most songbirds has been proven to vary geographically (Podos and Warren 2007), we hypothesized to observe some differences among geographically distant populations in both species. Analysis of data from coexisting populations of both *Locustella* species provides an opportunity to examine whether the same patterns of song geographic variation may be observed in closely related species at the same spatial scales.

Methods

Study species

Grasshopper and River Warbler are both common Palaearctic-African migrants (Cramp 1992; Cepák et al. 2008) with a patchy distribution across their large breeding ranges that overlap from western Germany to western European Russia (del Hoyo et al. 2006; Kennerley and Pearson 2010; Keller et al. 2020). Both species often coexist as they preferably occupy moist habitats with tall dense herbaceous vegetation, where they nest on the ground (Cramp 1992; Keller et al. 2020). Both Grasshopper and River Warbler are socially monogamous with bi-parental care (Cramp 1992; del Hoyo et al. 2006; Šťastný and Hudec 2011). In the studied Central European region, the overall male site fidelity is supported by re-trapping of 39 ringed adult males of the Grasshopper Warbler and 19 males of the River Warbler within a short distance of the original ringing site after one or more years (Cepák et al. 2008; Slovak Ringing Centre pers. comm.). It is noteworthy, however, that one River Warbler male was recaptured 73 km away, indicating some potential for dispersal of both genes and culture. Grasshopper Warbler males may apparently move also within the breeding season (Cramp 1992; D. Kerestúr pers. comm.). Data on site fidelity of yearlings in our study area are scarcer: only three re-captures of Grasshopper Warblers are available (all from the natal area) and none of River Warblers (Cepák et al. 2008; Slovak Ringing Centre pers. comm.).

Males of both Grasshopper and River Warblers are territorial, singing mostly at night (Cramp 1992; Šťastný and Hudec 2011). Despite being simple in general, songs of those two species differ in complexity, as apparent from publications providing example spectrograms. Their comparison, together with publicly available song recordings (Fig. S1 Supplementary Material 1), may provide some insights into the overall extent of their intraspecific song variation. However, neither within- nor among-population variability was studied in either of our study species.

The song of the Grasshopper Warbler consists of stereotypical repetition of one syllable containing two notes of varying bandwidth (Brackenbury 1978; Bergmann and Helb 1982; Glutz von Blotzheim and Bauer 1991; Cramp 1992; Kennerley and Pearson 2010) (Fig. 1a, b). This syllable with a typical frequency range of 4.5–8 kHz (Kennerley and Pearson 2010) is repeated at the rate of 22.5–31 syllables per second (Cramp 1992; Kennerley and Pearson 2010; Polakowski et al. 2013) for around 1 min (Schild 1986). Despite this low complexity, it has been demonstrated experimentally

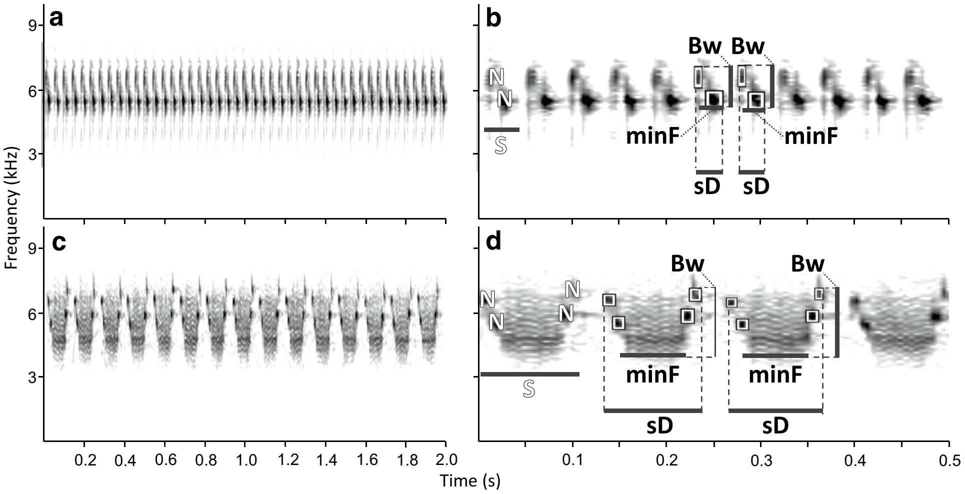


Fig. 1 Example spectrograms of the song of Grasshopper (**a**, **b**) and River Warbler (**c**, **d**): overview of 2 s and a detail of 0.5 s. Within the detailed views (**b**, **d**), quantitative characteristics of syllables (S) and notes (N) used in further analyses are highlighted: lowest frequency (minF) and bandwidth (Bw) as determined from the power spectra, peak frequency and peak time of notes (automatically measured within the manually outlined boxes in the spectrogram), and syllable duration (sD). Note that the maximum frequency, from which the bandwidth was calculated, was not equal to the peak frequency of the highest note in the syllable

that Grasshopper Warblers learn their vocalization (Becker 1990).

The song of the River Warbler is more complex, as demonstrated by visually distinct spectrograms included in various published sources (Bergmann and Helb 1982; Glutz von Blotzheim and Bauer 1991; Cramp 1992). A typical River Warbler song consists of one syllable containing 2–5 high-amplitude notes (Fig. 1c, d) but at least occasionally more complex songs are encountered, such as those composed of alternating pairs of syllables or even more complex syllable sequences (Bergmann and Helb 1982; Glutz von Blotzheim and Bauer 1991; Cramp 1992; Fig. S1 Supplementary Material 1). The syllables are repeated *ca* 7–16 times per second in a frequency range of 3–8 kHz for about 2 min (Mackowicz 1989; Cramp 1992; Kennerley and Pearson 2010; Polakowski et al. 2013). The rate, however, may to some extent vary among songs of the same individual (Glutz von Blotzheim and Bauer 1991; Cramp 1992), presumably reflecting male's motivation to attract the female (Mackowicz 1989).

Rarely, recordings of unusual River Warbler songs similar to other species, interpreted as vocal mimicry, were reported. These include, for example, a male singing similarly to the Great Tit (*Parus major*) in Finland (Bergmann and Helb 1982), and a male including occasionally in its vocalization a song typical for the Grasshopper Warbler in Poland (Polakowski et al. 2013). Vocal mimicry in the River Warbler vocalization indirectly demonstrates species' ability to learn song.

Fieldwork

To explore potential song variation among populations of both study species, we recorded *Locustella* males at four sites in Central Europe (Czechia and Slovakia), separated by 85–380 km (Table 1, Fig. 2a). The habitats at all localities were similar: moist meadows with fragments of open woodlands with dense herb cover, usually with beds of nettle (*Urtica*) and scattered willow (*Salix*), birch (*Betula*) or alder (*Alnus*) scrubs. At three of the sites, both study species co-occurred, with the River Warbler reaching higher population densities than Grasshopper Warbler. The latter species was completely absent from one of the localities (Poiplie). Altogether, we obtained recordings of 62 River Warbler males (10–20 per site) and 32 Grasshopper Warbler males (7–13 per site).

All recordings were collected at the beginning of the 2016 breeding season between the first week of May and the second week of June. Spontaneous songs of males of both focal species were recorded in stable weather conditions (no or little wind, no precipitation), using a Marantz PMD 661 digital recorder connected to a directional Sennheiser MKH 70 shotgun microphone. All tracks were recorded in 16-bit PCM format at a 44.1 kHz sampling rate.

Most recordings were obtained in the evening or early night (6 PM to 2 AM). In one of the localities (Uherské Hradiště), some of the males (3 out of 7 Grasshopper Warblers, and 15 out of 20 River Warblers) were also recorded in the mornings (5–9 AM); their song characteristics, however, did not differ substantially from those recorded at night. We always attempted to record a singing male from a distance of *ca* 5 m for 3 min. To avoid recording the same individual multiple times, territorial males were recorded at different parts of a given locality during each visit. Analysed recordings are accessible from the Animal Sound Archive at the Museum for Natural History in Berlin.

Song analyses

The recordings were first visually explored and analysed in the software Raven Pro v. 1.5.0 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY, USA). We filtered background noise using a bandpass filter to eliminate

Table 1 Position of studied localities, recording dates, number of recorded males, and range of syllable rates and their standard deviations within recordings from each population (median, minimum and maximum values are given)

Locality	Geographic position	Recording dates in 2016	Grasshopper warbler (*Locustella naevia*)			River warbler (*Locustella fluviatilis*)		
			n	Syllable rate (syllable/s)	Within-individual SD	*n*	Syllable rate (syllable/s)	Within-individual SD
Devínske jazero (SK)	48.30° N, 16.92° E	13, 21, 30 May; 8, 9, 15 Jun	12	23.8 (21.8–26.1)	0.18 (0.03–0.9)	12	8.3 (7.6–8.9)	0.08 (0.008–0.14)
Uherské Hradiště (CZ)	49.04° N, 17.55° E	20 May, 2 and 3 Jun	7	24.5 (23.4–26.1)	0.27 (0.10–0.82)	20	8.2 (7.5–9.1)	0.07 (0.007–0.24)
Poiplie (SK)	48.25° N, 19.61° E	14 and 15 May	0	N/A	N/A	20	8.0 (7.6–8.6)	0.06 (0.01–0.24)
Senné (SK)	48.68° N, 22.08° E	24, 25, 26, 27 May	13	23.1 (22.0–24.7)	0.08 (0.02–0.34)	10	8.1 (7.7–8.4)	0.02 (0.007–0.06)

Note that 1 out of 20 recorded river warbler males from poiplie sung atypical syllable category G (Fig. 2b), and its songs were not processed quantitatively

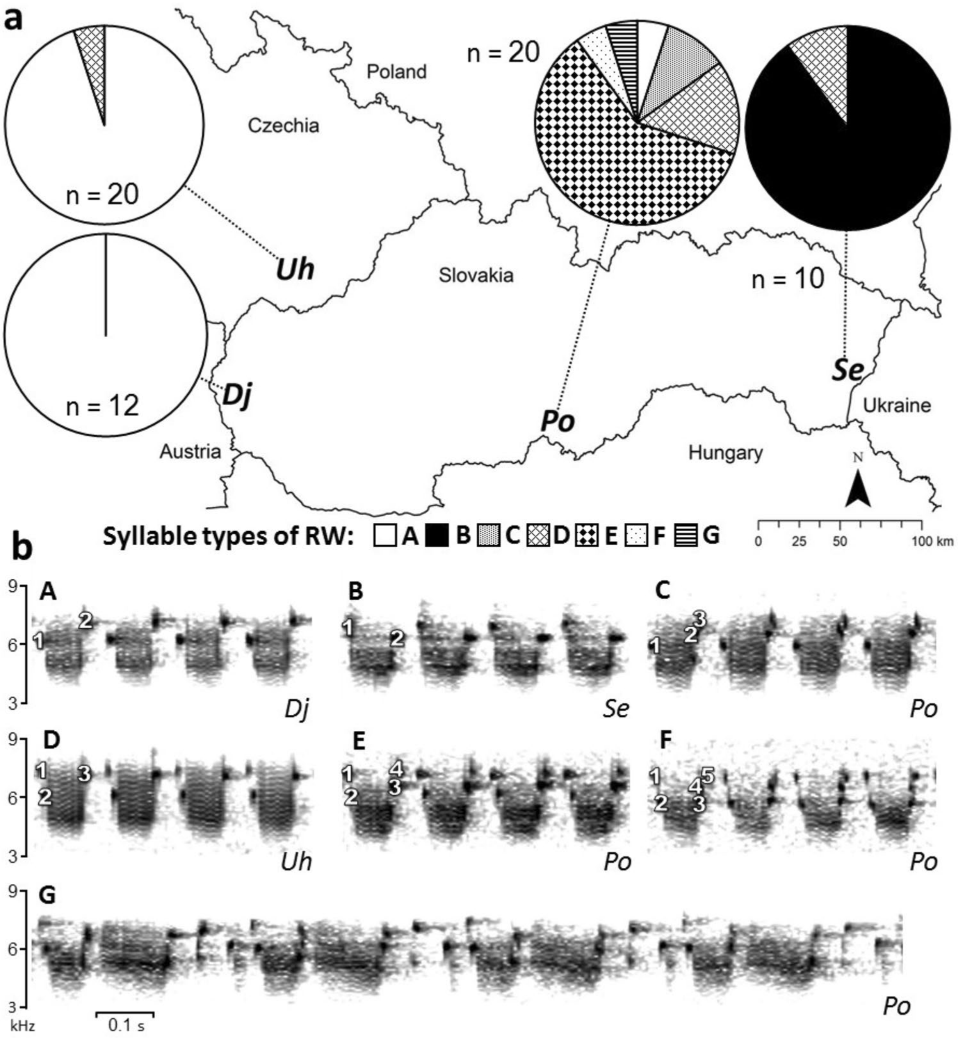


Fig. 2 Location of the recording sites: Uherské Hradiště (Uh), Devínske jazero (Dj), Poiplie (Po), Senné (Se), with the number of recorded River Warbler males and the proportion of River Warbler syllable categories for each site (**a**). Examples of four syllables of each syllable category of River Warbler, characterized by the number and position of high-amplitude notes (**b**). These notes are indicated by white numerals in the first syllable for categories A–F; syllables in the category G have incomparable structure

frequencies not interfering with the target bird song (above 9800 Hz and below 2800 Hz for the Grasshopper Warbler and above 9000 Hz and below 2800 Hz for the River Warbler). We excluded one River Warbler individual from all analyses because of its structurally aberrant song (syllable type G in Fig. 2b).

Considering that River Warbler males may modify their syllable rate up to two-fold when motivated to attract females (Mackowicz 1989), and presumably the same may be expected in other *Locustella* species, we quantified the syllable rates from three distinct parts of each recording to evaluate its potential variation. The lengths of these parts of song were chosen according to the overall syllable rate of the species: 40 syllables per a song for the Grasshopper Warbler, and 20 syllables per a song for the River Warbler. The syllable rate was quantified as the duration of the selected part of the song (including the gap following the last syllable) in seconds, divided by the respective number of syllables. Average values and standard deviations of the syllable rate were calculated for each male.

Subsequently, we removed from each recording the parts with loud noise or vocalization of other birds overlapping the target individual. Subsequently, we standardized the amplitude among these pre-processed recordings by equalizing the root-mean-square sound pressure in the individual WAV files (to maximize peak amplitude in every file), using the script "rms equalize" by Gabriël J. L. Beckers for the software PRAAT (Boersma and Weenink 2013). The equalized recordings were then processed in Raven Pro with the following settings: brightness: 50, contrast: 35, spectrogram window type: Hann, time grid overlap: 50, DFT size: 512.

The syllables were visually compared among males of each species separately. For River Warblers, we visually distinguished several song categories based on differences in the number of distinct notes and their position within a syllable (Fig. 2b). These differences were originally recognized on spectrogram printouts for which geographic origin was not indicated. Classification of recordings to the song categories was subsequently agreed upon by all authors.

Within recording of each male of both species, we randomly selected ten pairs of syllables (i.e., two consecutive syllables) of high quality, in which individual notes were clearly distinguishable (their peak power, as measured in the sound files after amplitude standardization in Raven Pro, exceeding the value of 80 dB relative to an arbitrary reference power). In each of these 20 syllables per male, we quantified the parameters indicated in Fig. 1b, d: number of notes, duration, lowest frequency and bandwidth (calculated as the difference between the highest and lowest frequency), and peak frequency and peak time within each note in the syllable. The lowest and the highest frequency of each syllable were measured from the power spectrum in the software Avisoft SASLab Pro v. 5.2.14 (Sound Analysis and Synthesis software, Berlin, DE), with a common threshold of − 18 dB relative to the syllable peak amplitude. This threshold, which encompasses 98.4% of the acoustic signal, was chosen based on the quality of recordings to consistently recover the bandwidth of the syllable but avoid impact of the background noise. Peak frequency and peak time within the notes were measured in Raven Pro in rectangular areas manually selected to outline each note in the spectrograms; in case, the same peak amplitude value occurred at various time or frequencies within the selection, the first time and lowest frequencies were automatically chosen. Position of a given note within a syllable was quantified as the relative position of the note peak time in respect to the duration of the whole syllable (i.e., ranging from 0 to 1). Recordings are available at https://doi.org/10.7479/54nv-qx50.

Statistical analyses

For each male, we calculated mean values of all quantified parameters (which, considering the uniformity of the species' song, well characterize the individual). The among-individual variation was then summarized in principal component analyses (PCAs) calculated separately for each species in Statistica v. 13.5 (TIBCO Software, Inc.). Due to the different complexity of the song between the species, the input variables (mean values of the characteristics listed above for each male) for the two PCAs differed. For the River Warbler, these included eight parameters: the number of recognizable notes in a syllable, syllable minimal frequency, bandwidth and duration, and peak frequency and relative peak time of the highest and the lowest note in each syllable (Fig. 1d). For the Grasshopper Warbler, we excluded two of those parameters: the number of notes, uniform across all males, and the peak frequency of the lower note, which was strongly correlated ($r = 0.89$) with the syllable minimal frequency.

To further assess the extent of among-population variation, and to identify which of the measured variables contribute most to the potential among-population differentiation, we performed a linear discriminant analysis separately for each species, based on the same input variables as PCAs. The grouping variable was the site identity, and we applied backward stepwise selection to choose the most informative parameters.

Summary data for each male, including average values for all measured variables, syllable rate and its standard deviation, as well as the first two principal components resulting from the respective PCAs, are provided as Supplementary Material 2.

Results

All recorded songs of Grasshopper and River Warblers from the study localities (except of the aberrant individual from Poiplie, Fig. 2b: G) consisted of one repeated syllable, homogeneous within the song of a given individual. The recorded songs were sung within a relatively narrow range of syllable rates (average values of individual males from 21.8 to 26.1 syllables per second for Grasshopper Warblers, and 7.5–9.1 for River Warblers), with negligible within-individual variation (Table 1; Supplementary Material 2).

Based on visual inspection of spectrograms, we divided syllables sung by River Warbler males into seven categories based on the number of distinguishable notes (2–5) and their relative position in the spectrograms (Fig. 2b). The distribution of these song categories among studied populations was very uneven; in each location, one such category was dominant, sung by the majority of males (Fig. 2a).

In the two populations located in the western part of the study area (Devínske jazero and Uherské Hradiště), most males sang two-note syllables with the first note of a lower frequency than the second one (category A; Fig. 2b), which was also recorded in one male in Poiplie. The majority of males in the easternmost locality Senné sang another two-note song category with a high-frequency first note (B); we observed this category only in that population. In Poiplie, all but one male sang syllables containing three or more notes; most of them used four-note syllables (category E) but we distinguished altogether six categories in that population based on the number and position of notes within the syllable. Four of these (C, E, F, and the aberrant type G) were recorded only in Poiplie. A three-note syllable category D was not dominant in any of the studied populations but males singing it were recorded at three sites: apart from three males from Poiplie, one was recorded in Uherské Hradiště and another one in Senné (Fig. 2a).

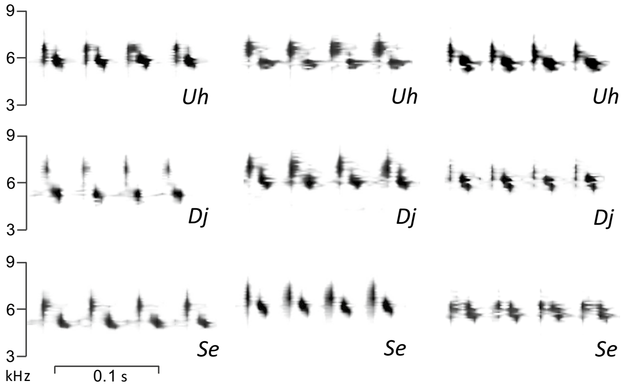


Fig. 3 Examples of four syllables of nine Grasshopper Warbler males. Male origin is indicated in the lower right corner of each spectrogram: Uherské Hradiště (Uh), Devínske jazero (Dj), Senné (Se)

No such categorization was possible for the recorded Grasshopper Warbler songs. The syllables were always double-noted, with higher frequency note followed by a lower frequency note, slightly varying in relative frequency and power distribution of the notes among the males (Fig. 3). This prevented us from classifying the Grasshopper Warbler songs into distinct categories. Song variants with visually similar spectrograms re-occurred among the locations.

The first two principal components in PCAs captured over 56% of the overall variation in the data for the Grasshopper Warbler, and over 61% for the River Warbler (Fig. 4). The patterns of population differentiation contrasted between the two species, reflecting the observed variation and distribution of the syllable types. In the Grasshopper Warbler, points representing males from different populations were scattered among each other (Fig. 4a).

This was not the case for the River Warbler; where most individuals from the two easterly located populations (Poiplie, Senné) formed clearly separate clusters, and only those from the two western populations (Uherské Hradiště, Devínské jazero) partially overlapped (Fig. 4b). Points representing two males from Uherské Hradiště and Senné singing three-note syllables were distinctly separated from the others of the respective populations. However, the scatter in PCA only partly corresponded to our categorization of syllable categories in this species (Fig. S2, Supplementary Material 1). While the males singing two-note syllable categories A and B formed separate clusters, those singing categories with three or more notes (all but two from Poiplie) were mixed, reflecting variation in other frequency and temporal characteristics of the males' vocalization.

The discriminant analyses confirmed the patterns apparent from the PCA results. For the Grasshopper Warbler, the analysis failed to reveal any tendency for population differentiation. The discriminant analysis did not yield significant patterns, and no variable was retained in the model during the backward selection procedure. In contrast, for the River Warbler, the backward selection retained three variables (the number of notes, and the frequency and relative position of the lowest note within the syllable) in the model, which was highly significant (Wilks' Lambda: 0.0152, approx. F $(9,134) = 68.25$, $p < 10^{-4}$). When the a priori probability for classification was set equal for all sites, this model successfully classified 80% of individuals to their respective population, misplacing mostly males from the western populations (Uherské Hradiště, Devínske jazero), one male from Senné (singing locally unusual three-note syllable category D), and one male from Poiplie (singing locally unusual two-note syllable category A).

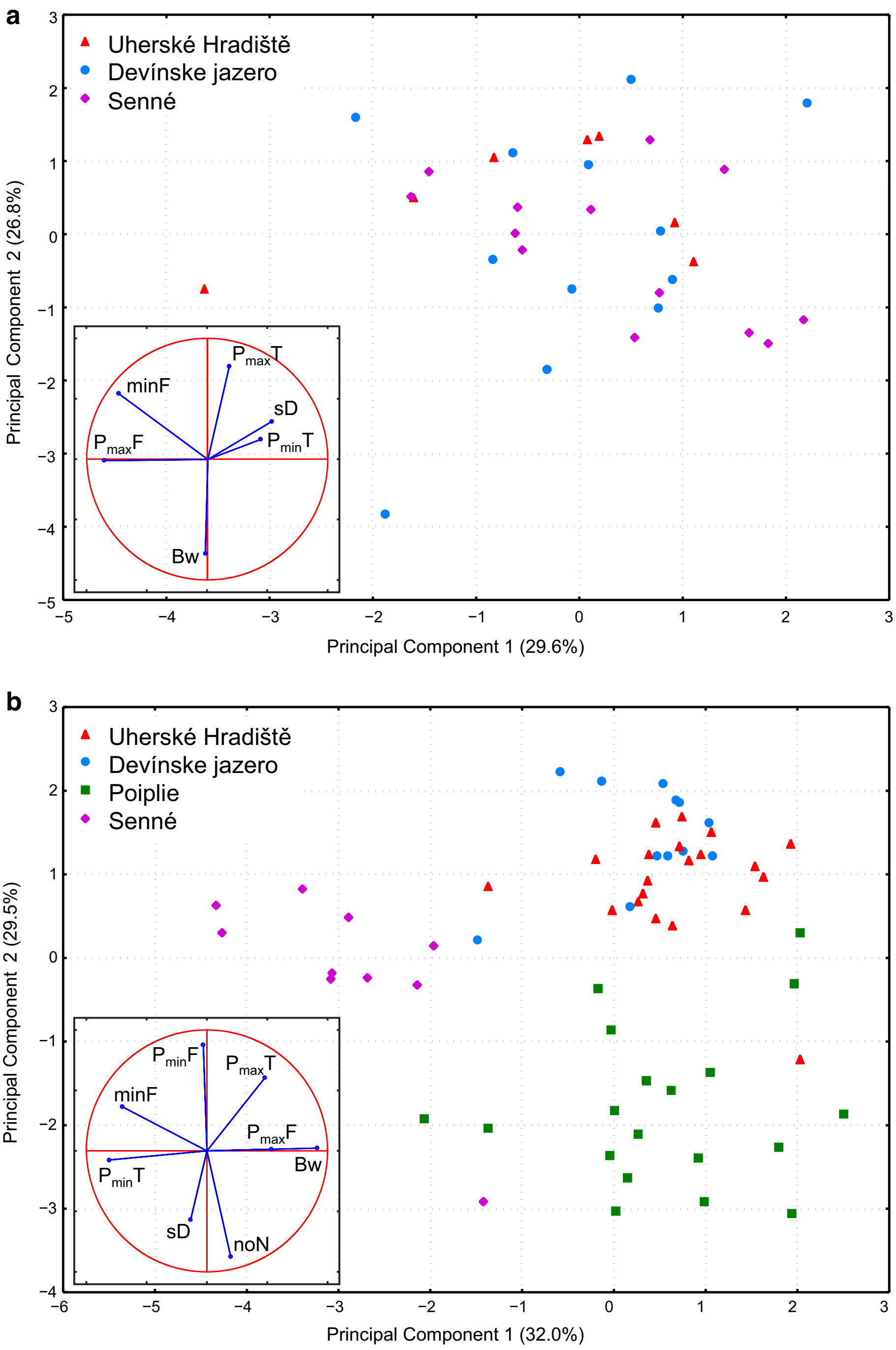
Discussion

Contrary to our expectations, the patterns of song geographic variation of Grasshopper and River Warblers greatly differed between the two species. Songs of the Grasshopper Warbler did not vary among the studied populations, but those of the River Warbler showed at the same spatial scale a clear pattern of geographic divergence. The four studied populations could be differentiated to three groups based on the dominant song categories. The discriminant analysis based on quantitative temporal and frequency characteristics was in concordance with our subjective classification of River Warbler songs: all three variables retained after the backward selection characterized the number and position of selected high-amplitude notes in the syllable, i.e., the features used by us to define song categories. Other measured frequency or temporal characteristics did not show consistent among-population differentiation. In particular for syllable duration, lack of such differences was not surprising. All analysed songs were sung at rates typical for the species' territorial songs (Cramp 1992; Kennerley and Pearson 2010; Polakowski et al. 2013), however, it might be expected that syllable duration may vary when males modify syllable rates.

The differences found in River Warbler songs among our observed localities are not unusual, as the songs of oscine passerines often vary geographically even in species with a simple song, such as in the Swamp Sparrow (*Melospiza georgiana*) (Marler and Pickert 1984; Balaban 1988), Yellowhammer (*Emberiza citrinella*) (Wonke and Wallschläger 2009; Diblíková et al. 2019) and White-crowned Sparrows (*Zonotrichia atricapilla*) (Shizuka et al. 2016). This variation, however, contrasts with the pattern observed in the conspecific Grasshopper Warbler where similar songs largely reoccurred among studied populations.

The differences between the studied species in geographic variation of vocalization are even more obvious when recordings from different locations in Europe (Fig. S1,

Fig. 4 Principal component analyses with projection of the variables of songs of 32 Grasshopper Warbler males (**a**) and 61 River Warbler males (**b**). Each point represents the song of one male and different symbols represent different populations. Abbreviation of variables: *noN* number of notes in a syllable, *minF* low frequency, *Bw* frequency bandwidth, *sD* syllable duration, $P_{max}F$ peak frequency of the highest note in each syllable, $P_{min}F$ peak frequency of the lowest note in each syllable, $P_{max}T$ relative peak time of the highest note in each syllable, $P_{min}T$ relative peak time of the lowest note in each syllable. Eigenvalues of correlation matrices and associated statistics are provided as Supplementary Table S2 in Supplementary Material 1



Supplementary Material 1) and spectrograms published in various sources (Bergmann and Helb 1982; Glutz von Blotzheim and Bauer 1991; Cramp 1992) are considered. A simple visual inspection of recordings of River Warbler males revealed many more distinct song variants than found in our study. Apart from those detected at our four localities, some recordings on a wider range show for example the songs composed of repetition of a group of structurally different syllables or, less commonly, there is an element incorporated between the successive syllables (Fig. S1, Supplementary Material 1). On the contrary, Grasshopper Warbler song variants detected in our study were visually similar to those across other parts of European breeding range of this species (Fig. S1, Supplementary Material 1).

In many passerine species, conspecific males from the same locality tend to share song types or song structures, often as a result of male–male interactions in which song sharing might ease the communication among neighbours (Todt and Naguib 2000; Griesmann and Naguib 2002; Beecher and Brenowitz 2005); but other species do not exhibit any such sharing (e.g., Morton and Young 1986; Tsipoura and Morton 1988; Liu and Kroodsma 2006). Even when diverse song variants persist across species' breeding range, consistent patterns of geographic variation may occur, e.g., in temporal variation (Searfoss et al. 2020). Although we cannot exclude some spatial trends in quantitative song parameters at a larger scale for the Grasshopper Warbler, it was not the case of our studied populations.

Besides the male–male interactions, intraspecific song variation can also be influenced by female preferences, as female choice may lead to local song uniformity (e.g., O´Loghlen and Rothstein 1995; Searcy et al. 2002). In many bird species, female preferences for fast trills, which may serve as male quality signal, were documented (e.g., Vallet and Kreutzer 1995; Ballentine et al. 2004). Simple songs of some *Locustella* species, such as the Grasshopper Warbler, resemble fast trill structures found in vocalization of other songbirds, and female preferences might have driven the overall fast rate rather than complexity of this species' song. In contrast, distinct variation of the River Warbler could be influenced from female preferences for common local song variants. To test such hypotheses, however, direct experiments focusing on female response to various acoustic stimuli would be needed.

Apart from social interactions, intraspecific geographic variation of song may be affected by population dynamics (e.g., Podos and Warren 2007; Catchpole and Slater 2008) and connectivity. Dispersal of young birds may result in song uniformity among populations in non-migratory species (Kroodsma et al. 1999a). Both Grasshopper and River Warblers in our study region are both migratory (Danko et al. 2002; Šťastný and Hudec 2011), but they seem to differ in population dynamics within a breeding season. In one thoroughly monitored Slovak population (on the area of 14 ha where all singing males got ringed), the density of breeding pairs of Grasshopper Warbler increased by 25% after the first breeding, because new males, presumably young ones, had joined the population. No such change was observed for River Warblers monitored in the same area (D. Kerestúr pers. comm.). Fluctuations in the number of singing males is also mentioned for Bavarian populations of Grasshopper Warbler (Cramp 1992). This indicates that the populations of this species, at least in Central Europe, may be more interconnected than those of the River Warbler. An increased male dispersal could then contribute to mixing of song types in the former species, in contrast with the observed geographic variation of song that we observed in the latter.

The similarity of songs in the two studied western populations of the River Warbler (Uherské Hradiště and Devínske jazero), observed both at the level of assignment of song to categories (Fig. 2) and in quantitative parameters (Fig. 4b), indicates that the level of among-population differentiation may vary across the species' range, likely reflecting the increased population connectivity or a homogeneous sharing of acoustic features in that region. It is even possible that some features of River Warbler songs change in space abruptly and song categories recognized by us are distributed in a mosaic fashion (as, e.g., Yellowhammer dialects in Central Europe; Diblíková et al. 2019). The observed rare occurrence of song categories common elsewhere might be explained by occasional male dispersal over longer distances, but other processes such as an independent convergent emergence of a similar variant during song learning or local temporal fluctuations of frequency of song categories, cannot be excluded. Interestingly, within the River Warbler populations studied by us, the largest variation in song characteristics but also largest structural complexity within songs (as seen in the number and distribution of notes within syllables) was observed in Poiplie, a site located approximately half-way between the populations where simpler but distinctly different song categories with two-note syllables dominated. More complex song categories with a higher number of notes could possibly emerge as a combination of features of the simpler ones when birds singing these variants got into contact. However, much more detailed spatial data would be necessary to evaluate these scenarios.

The song geographic variation may also be affected by the habitat inhabited by the respective bird populations, which may adapt their quantitative song characteristics to optimize sound transmission in different environments (e.g., Morton 1975; Wiley 1991). Furthermore, patterns of song sharing may be influenced by the extent of habitat fragmentation (Briefer et al. 2009; Laiolo and Tella 2005). Neither of these processes, however, can explain differences between species observed in our study. Both *Locustella* species have similar habitat preferences, and they coexisted at three of the studied localities. Furthermore, the local habitat characteristics were similar among all four sites where we recorded the River Warbler songs. It is possible, however, that the higher similarity between the two studied westerly located populations of that species was affected not only by the geographic proximity but also by the distribution and fragmentation of suitable habitats.

Of course, various mechanisms affecting the geographic variation of the song are not mutually exclusive. Xing et al. (2017) explored the spatial song variation in a congeneric species, the Marsh Grassbird (*Locustella pryeri sinensis*), along the latitudinal gradient in eastern China, over a distance exceeding 2000 km. They speculated that the observed differences may have been influenced by both the intensity of sexual selection (increasing from the southern sedentary populations towards the northern migratory ones) and the differing climates influencing the local vegetation structure and weather conditions. It is noteworthy, however, that the Marsh Grassbird, despite belonging to the genus *Locustella*, is more divergent from both our studied species (belonging to another main clade within the genus; Alström et al. 2018), and exhibits more complex vocalization comprising two distinct song parts (Xing et al. 2017).

Although the contrast observed between the two coexisting *Locustella* species was unexpected, differences in the song geographic variation among congeneric species are not exceptional. For example, within the American crowned sparrows (*Zonotrichia* spp.), gradual changes of a simple song of the White-throated Sparrow (*Z. albicollis*; Ramsay and Otter 2015) contrast with the dialect patterns found in more complex songs of various subspecies of the White-crowned Sparrow (*Z. leucophrys*; e.g., Marler and Tamura 1962; Baptista 1977; Baptista and King 1980; Chilton et al. 2002) and the Golden-crowned Sparrow (*Z. atricapilla*; Shizuka et al. 2016).

By showing that the patterns of song geographic variation differ among the two coexisting closely related *Locustella* species with the same habitat preferences, we further highlight the great diversity of songbird vocalization. Our results imply that the factors contributing to song divergence can be species-specific even in related sympatric taxa with a simple song.

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Author contributions IC, LR and TP designed the study. IC and LR recorded the songs in the field. IC performed bioacoustic analyses. AP performed most data analyses. All authors contributed to the manuscript writing.

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Availability of data and material Analysed songs will be provided via the Journal of Ornithology sound library.

Declarations

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