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Song divergence of two Bluethroat subspecies (*Luscinia s. svecica* and *L. s. cyanecula*)

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As birds adapt to changing biotic and abiotic environmental conditions, parameters of their acoustic signals are modified by selective pressure for efficient communication. Such changes in song features may result in acoustic divergence among populations of the same species. We studied the divergence of songs in four populations of two genetically distinct subspecies of the Bluethroat *Luscinia svecica* – *L. s. svecica* and *L. s. cyanecula*. Males of *svecica*, occupying tundra habitats, produced less diverse songs with lower frequencies than *cyanecula* males occurring in several types of habitat. The differences in frequency parameters may be related to larger body size of the former subspecies; however, habitat associations predict an opposite relationship. Contrary to expectations, repertoire size did not significantly differ between the two subspecies, although *cyanecula* inhabits habitats with higher density and diversity of songbirds (which it may imitate). Temporal song parameters (song length, pause length, and song rate) differed significantly among populations but not between subspecies. Differences in song characteristics might be important in subspecies recognition, and may therefore contribute to the maintenance of subspecific differences or even influence the speciation process.

1. Introduction

Many bird species use simple calls with repeatable structure that are similar among individuals, while others perform long, complex songs that are clearly individually characteristic despite having some species-specific characteristics (Catchpole & Slater 1995). The songs of songbirds are of particular interest, as they are transmitted culturally and play a crucial role in sexual selection by acting as a rival deterrent and/or mate attractor (Kroodsma & Byers 1991).

In some species, song variability among populations develops across very short distances and local dialects may have distinct boundaries (e.g., McGregor 1980). In other species, geographic variation is not as apparent, and songs change gradually over long distances (e.g., Searcy *et al.*

2002). Several mechanisms might play a role in acoustic divergence.

Birds use various techniques to enhance song transmission and minimize degradation (Wiley & Richards 1982). For instance, they may adjust song frequency to avoid song degradation caused by the physical structure of their habitats (acoustic adaptation hypothesis; Morton 1975) or ambient noise (Badyaev & Leaf 1997). Increasing the length or repeating a song provides a more redundant signal for communication over long distances (Sorjonen 1986a).

Also morphological differences can shape frequency parameters. Many studies have found a negative correlation between body size and the frequencies used in song (Ryan & Brenowitz 1985, Tubaro & Mahler 1998, Kipper *et al.* 2006). Moreover, in terms of production, sounds with low frequency are more costly for small than for large birds (Tubaro & Mahler 1998, Bertelli & Tubaro 2002).

Other processes that may potentially affect song diversity are intra- and inter-sexual selection. Increased intensity of male-male interactions caused by high densities at breeding sites may result in changes to song characteristics such as song length (Galeotti *et al.*1997, Gil *et al.* 2007), song rate (Olinkiewicz & Osiejuk 2003, Chiver *et al.* 2008) and even song composition (Griessmann & Naquib 2002, Suter *et al.* 2009). Inter-sexual selection mostly influences repertoire size (Lampe & Saetre 1995, Hasselquist *et al.* 1996, Hosoi *et al.* 2005, Nicholson *et al.* 2007). The size of a repertoire is constrained by song sharing among neighbours and/or differential preferences of females for specific (usually local) motives of male songs (Vaneechoutte 1997, O'Loghlen & Beecher 1999, Beecher *et al.* 2000, Grießmann & Naguib 2002, Searcy *et al.* 2002). All these factors may increase signal differences between populations and reinforce species recognition through learned female preferences (Irwin & Price 1999). Selection for species recognition may cause reproductive isolation in populations through signal divergence (Slabbekoorn & Smith 2002), which might play an important role in speciation (Irwin & Price 1999).

The existence of subspecies complexes is useful for detecting and describing the speciation process at an early stage. One such model group is the Bluethroat (*Luscinia svecica*) subspecies complex, consisting of ten recognized subspecies that differ in, e.g., body size and wing length (Eybert *et al.* 1999, Arizaga *et al.* 2006), throat ornamentation (Johnsen *et al.* 2006) and breeding-habitat (Cramp 1988). Microsatellite genotyping indicated a well-differentiated southern group of subspecies with a white or absent throat spot, into which the Central European subspecies *L. s. cyanecula* belongs, and an undifferentiated northern group of putative subspecies with a red throat spot that includes the nominate subspecies *L. s. svecica* (Johnsen *et al.* 2006). These groups likely diverged over the past 15,000 years (Zink *et al.* 2003). In the present study, we focused on songs of the two above-mentioned subspecies, i.e., *svecica* and *cyanecula*.

Bluethroat males have a complex song which is often performed in flight (Armstrong & Westfall 1953, Sorjonen 1986b, Cramp 1988). The beginning of the song is markedly stereotypical, while the ending is more variable and individually specific (Cramp 1988). Generally, birds of the genus *Luscinia* produce songs of large repertoire (Sorjonen 1986b). Additionally, Bluethroat males are able to imitate songs of other bird species (Cramp 1988). A detailed visual inspection of sonograms has revealed that males usually sing a set of often-repeated elements, and then consecutively add new elements in succession during the song (Naguib & Kolb 1992).

The aim of the present study was to examine variation in characteristics of Bluethroat vocalization at subspecies and population levels, by comparing four geographically distinct populations of Bluethroat subspecies *svecica* and *cyanecula* that require different breeding habitats and partly occupy different biogeographic regions.

2. Material and methods

2.1. Study area

Fieldwork was carried out during breeding seasons (April–June, 2006–2009) at four localities. Songs of *svecica* were studied in the Giant Mountains (Czech Republic, 50° 44' N, 15° 42' E, 1,400 m a.s.l.) and in the Abisko region (Sweden, 68° 21' N, 18° 48' E, 370 m a.s.l.). The study area in the Giant Mountains consists of wet alpine meadows

Table 1. Definitions of acoustic variables, divided into spectral, temporal and structural parameters and repertoire size, estimated for the studied Bluethroat songs.

Parameter type	Variable	Definition
Spectral	Highest F	Upper frequency bound of the song
	Lowest F	Lower frequency bound of the song
	F-bandwidth	Difference between high and low frequencies of the song
Temporal		
	Song length	Time between the start and end of the song
	Pause length	Time between two songs
	Song rate	Number of songs per minute
Structural		
	Syllable rate	Number of syllables per song
	Transition rate	Number of transitions in a song of given length
	Transitions	Number of switches between syllable types within a song
	Versatility	Number of transitions divided by the maximal potential number of transitions in a song of given length
	Diversity	Number of syllables per song divided by the number of syllable types per song
Repertoire size		Cumulative number of different syllable types for 5 minutes

and peat bogs partially covered by dwarf pine (*Pinus mugo*) and solitary Norway spruce (*Picea abies*). The Abisko region is situated about 200 km north of the Arctic Circle, with arctic tundra habitat consisting of bogs partially covered by scrub vegetation.

Songs of *cyanecula* were recorded at the Třeboň region in southern Czech Republic (49° 05’ N, 14° 45’ E, 430 m a.s.l.) and the area of Noteć river valley and Nadnoteckie Łęgi (53° 1’N, 16° 33’E, 40 m a.s.l.) in north-western Poland. In the Třeboň region, Bluethroats inhabit dense reed vegetation overgrowing banks of large fish ponds; in the Noteć river valley, typical Bluethroat habitats are surroundings of oxbow lakes and flooded peat-pits.

2.1. Recordings and song analysis

Recordings of the males of both subspecies were obtained using a Marantz PMD 222 3-head mono tape recorder, Sennheiser MKH 70 or MKH 50 directional microphones, and SONY UX-S 60 audio tapes. Males of *svecica* were individually identified by colour rings. For *cyanecula*, however, not all individuals were colour ringed; therefore, each male was recorded only once to avoid pseudoreplication. We usually recorded males from a distance of 1–30 m for 5–10 minutes. Songs were recorded during days free of precipitation, in variable daytime and weather conditions (in terms of temperature, wind and cloud cover).

The recordings were transferred from the Marantz recorder via a shielded analogue cable to a PC equipped with a Sound Blaster Audigy 2 sound card, and digitalised using 44.1 KHz/16 bit sampling. Further analyses (time and frequency measurements) were done in Avisoft SAS Lab Pro version 4.40 (Specht 2007) and Raven 1.4 software (www.birds.cornell.edu/raven).

To measure spectral (highest frequency, lowest frequency, frequency bandwidth) and temporal characteristics (song length, pause length, song rate), sonograms of song recordings obtained from 84 birds were initially used (*cyanecula*: 24 males from Třeboň and 12 males from Noteć; *svecica*: 33 males from the Giant Mountains, 15 males from Abisko). To examine the structural characteristics of songs, sonograms of 5-min continuous song bout samples, randomly selected from high-quality recordings, were prepared for individual males. This procedure reduced the sample size to 50 recorded males (*cyanecula*: 12 Třeboň, 12 Noteć; *svecica*: 13 the Giant Mountains, 13 Abisko).

Songs of these 50 individuals were described by syllables defined as representing the smallest invariant units in the song. A visual inspection of sonograms from all selected individuals was carried out, and song structure was described. For each 5-min sample (15–30 songs), the number of syllables per song, the number of different syllables (syllable types) per song, and the cumulative number of syllables per song bout, were counted. The number of transitions (syllable variability), transition rate, syllable rate, versatility and diversity were calculated from the above parameters. As repertoire size might be important for an imitative bird with complex song (such as the Bluethroat), the cumulative number of different syllable types (repertoire size) per 5-min song bout were measured for males of the Czech populations. All measured song parameters are given in Table 1.

2.2. Statistical analyses

In the first step, the distribution of all variables was examined and data were then subjected to parametric or non-parametric tests as appropriate. ANOVA or Kruskal-Wallis test (with Bonferroni probability adjustments) with subsequent Bonferroni *post hoc* tests were used to test for significant differences in song characteristics between studied populations and subspecies. Because the number of recorded songs per male differed (a total of 2253 songs from 84 males belonging to four populations; on average 26.40 ± 1.29 SE songs per male), mean values of song characteristics from each male were used in these analyses. All statistical analyses were conducted using SPSS v.16.

Furthermore, the body measures obtained from males from two study populations in the Czech Republic were compared using *t* test and the Mann-Whitney *U* test. In these analyses, data collected during six years field work (2000–2006) were used; many males were measured but not recorded in that period. As all recorded *cyanecula* males could not be captured for measurements, the data set of body measurements and song parameters was insufficient for a detailed analysis. Therefore, only the complete data set obtained from the Czech *svecica* population ($N = 13$) was used to evaluate if the overall song frequency is affected by male body mass. For this analysis, frequency variables were combined into one principal component (PC1) that represented approximately 95% of the variation in the original variables (Table 2); the data appeared to be well suited for such an analysis (Kaiser-Meyer-Olkin measure of sampling adequacy 0.847, Bartlett's test of sphaericity 78.323). Linear regression was subsequently used to test the potential relationship between bird size and song frequencies.

Table 2. Eigenvalue, variance explained and weightings of the original variables in the first principal component extracted from the original spectral Bluethroat song variables.

Statistics and original spectral variable	PC1
Eigenvalue	3.819
Percent of variance	95.471
Cumulative percent	95.471
Variables	
Q1 frequency	0.972
Q3 frequency	0.957
Center frequency	0.992
Peak frequency	0.986

The frequency variables measured in Raven software were (i) 1st Quartile Frequency, and (ii) 3rd Quartile Frequency = the frequencies that divide the syllable into two frequency intervals containing 25% and 75% of the energy, or 75% and 25% of the energy, respectively; (iii) Peak Frequency = the frequency at which maximum power occurs within the syllable; and (iv) Center Frequency = the frequency that divides the syllable into two frequency intervals of equal energy. Because intra-sexual selection (male-male interactions) may possibly affect song parameters, the density of singing males at breeding sites was compared. The density was defined as being the number of neighbours for each singing male, and was compared only between the Czech populations using Mann-Whitney *U* test.

3. Results

3.1. Spectral characteristics

The songs of Bluethroat males significantly differed among the four populations in highest frequency ($F_{3,80} = 15.56$, $P < 0.001$), lowest frequency ($F_{3,80} = 7.45$, $P < 0.001$) and frequency bandwidth ($F_{3,80} = 7.97$, $P < 0.001$). In terms of the highest frequency, Bonferroni *post hoc* tests re-

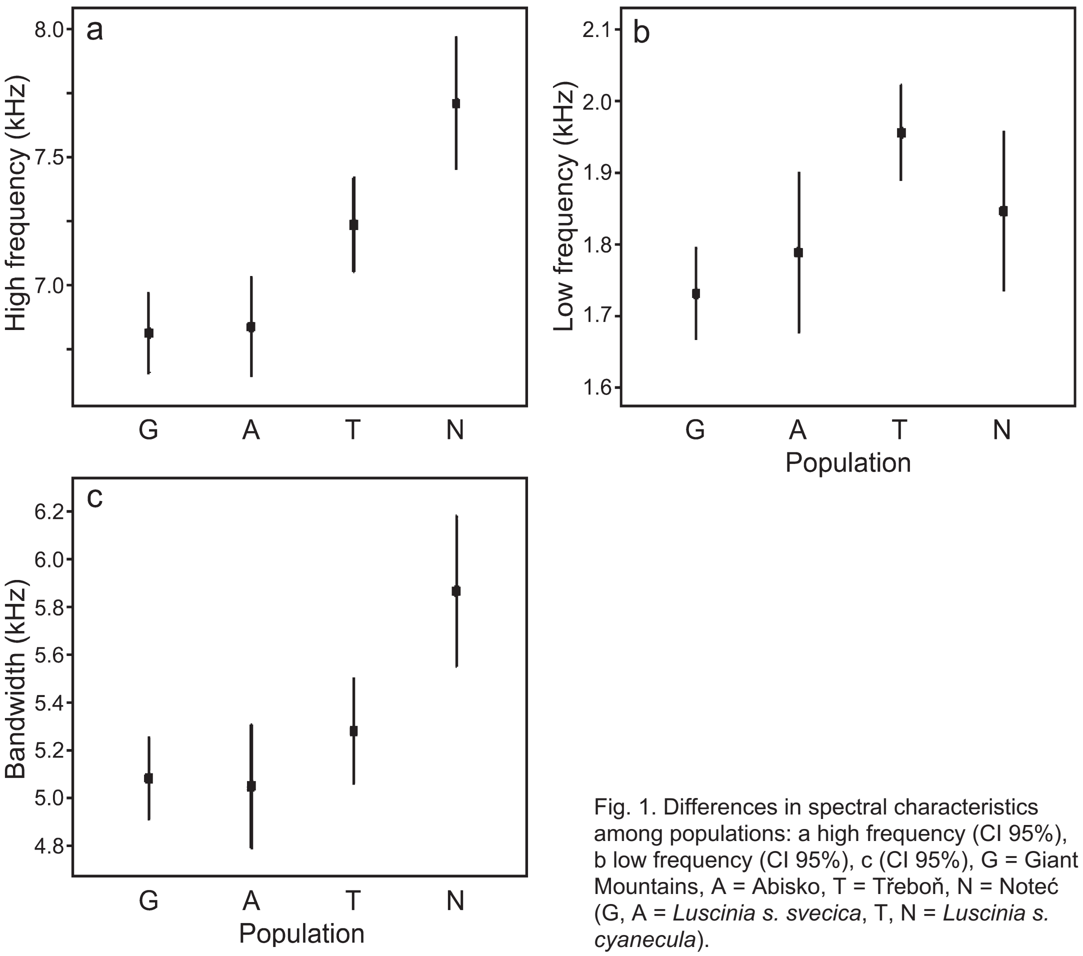

Fig. 1. Differences in spectral characteristics among populations: a high frequency (CI 95%), b low frequency (CI 95%), c (CI 95%), G = Giant Mountains, A = Abisko, T = Třeboň, N = Noteć (G, A = *Luscinia s. svecica*, T, N = *Luscinia s. cyanecula*).

vealed that only the Giant Mountains and Abisko populations did not significantly differ from each other (Fig. 1a). In terms of the lowest frequency, the Třeboň population significantly differed from those of the Giant Mountain ($P < 0.001$) and Abisko ($P = 0.036$). The Noteć population, however, did not significantly differ from the other populations in this parameter (Fig. 1b). On the other hand, the *post hoc* test showed that the Noteć population significantly differed from all the other populations in frequency bandwidth ($P \leq 0.01$ for all pair-wise comparisons; Fig. 1c).

3.2. Body size

Body measurements collected during six seasons in two Czech populations representing both sub-

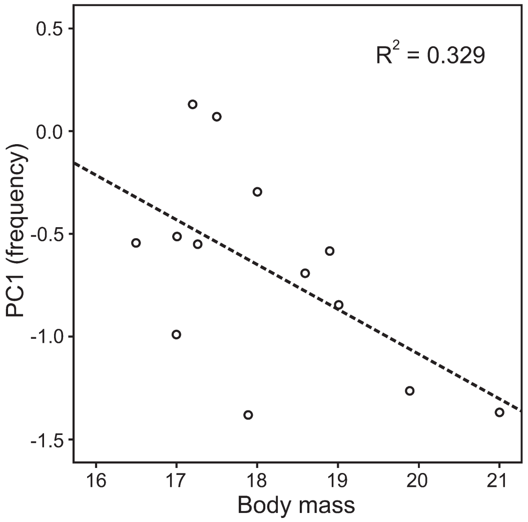

Fig. 2. PC1 (i.e., song frequency) negatively correlates with body mass.

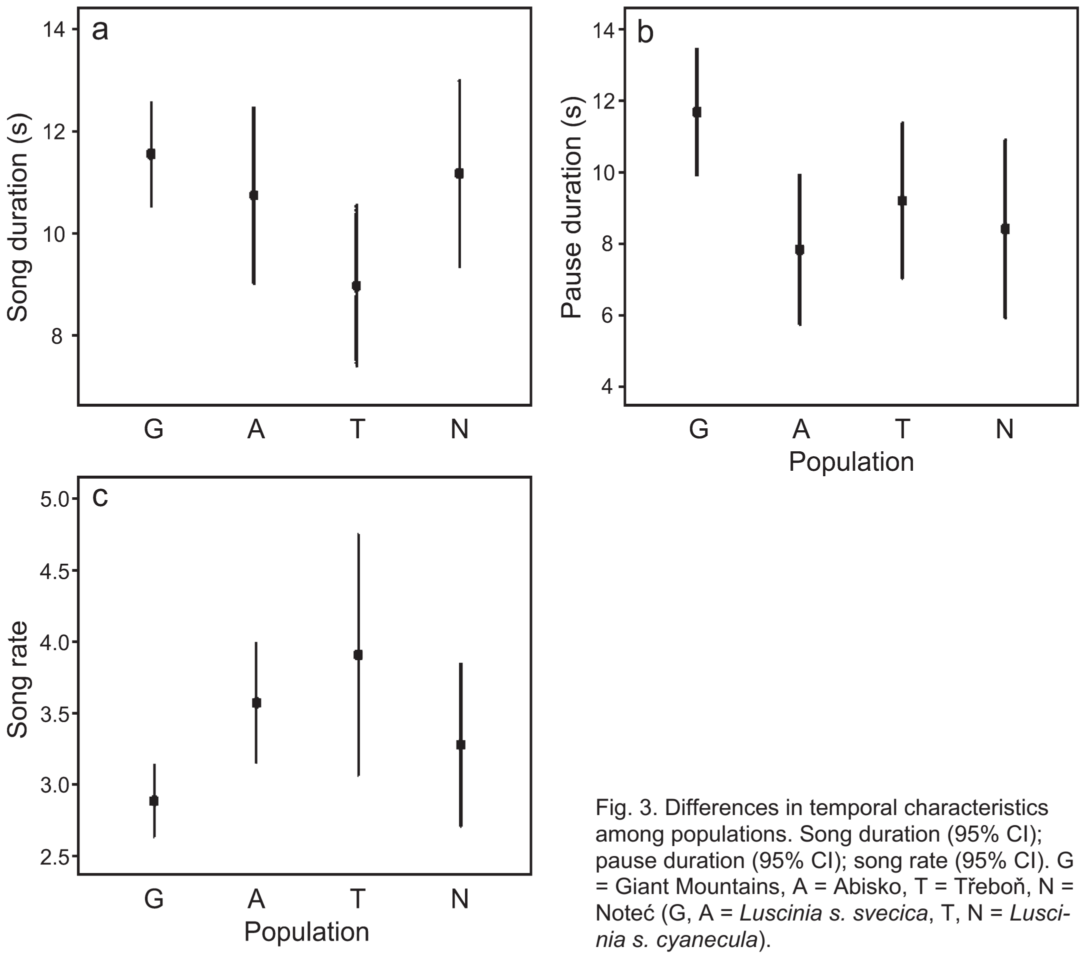

Fig. 3. Differences in temporal characteristics among populations. Song duration (95% CI); pause duration (95% CI); song rate (95% CI). G = Giant Mountains, A = Abisko, T = Třeboň, N = Noteć (G, A = *Luscinia s. svecica*, T, N = *Luscinia s. cyanecula*).

species were analyzed. Males from the Giant Mountains *svecica* population were significantly larger than those from the Třeboň *cyanecula* population in terms of wing length (t_{107}= 5.341, $P <$ 0.05), tail length (t_{107} = –2.343, $P < 0.05$), tarsus length (t_{107} = 5.083, $P < 0.05$) and body mass (t_{107} = 3.539, $P < 0.05$). However, bill length did not significantly differ between the two populations (t_{107} = 1.244, $P = 0.656$).

The effect of body mass on song frequency was tested only for the Czech *svecica* males from the Giant Mountains. Linear regression showed a significant negative correlation between body mass and PC1 (i.e., the frequency parameters) (R = 0.332, $F = 5.388$, $P < 0.05$, $N = 13$; Fig. 2).

3.3. Temporal characteristics

Song length (duration) and song rate significantly differed among Bluethroat populations ($F_{3,80}$ = 3.12, $P <$ 0. 05 and $F_{3,80} = 3.22$, $P < 0.05$, respectively) and these two parameters were negatively correlated (Pearson's $r = – 0.438$, $P < 0.01$, N = 84). Subsequent Bonferroni *post hoc* tests showed significant differences in song length ($P = 0.024$) and song rate ($P = 0.020$) between the *cyanecula* population from Třeboň and the *svecica* population from the Giant Mountains (Figs. 3a, 3c). Males in the Třeboň population tended to sing slightly shorter songs than did males of the other populations (Fig. 3a). Pause length did not significantly differ among populations (Fig. 3b), although males from the Giant Mountain population

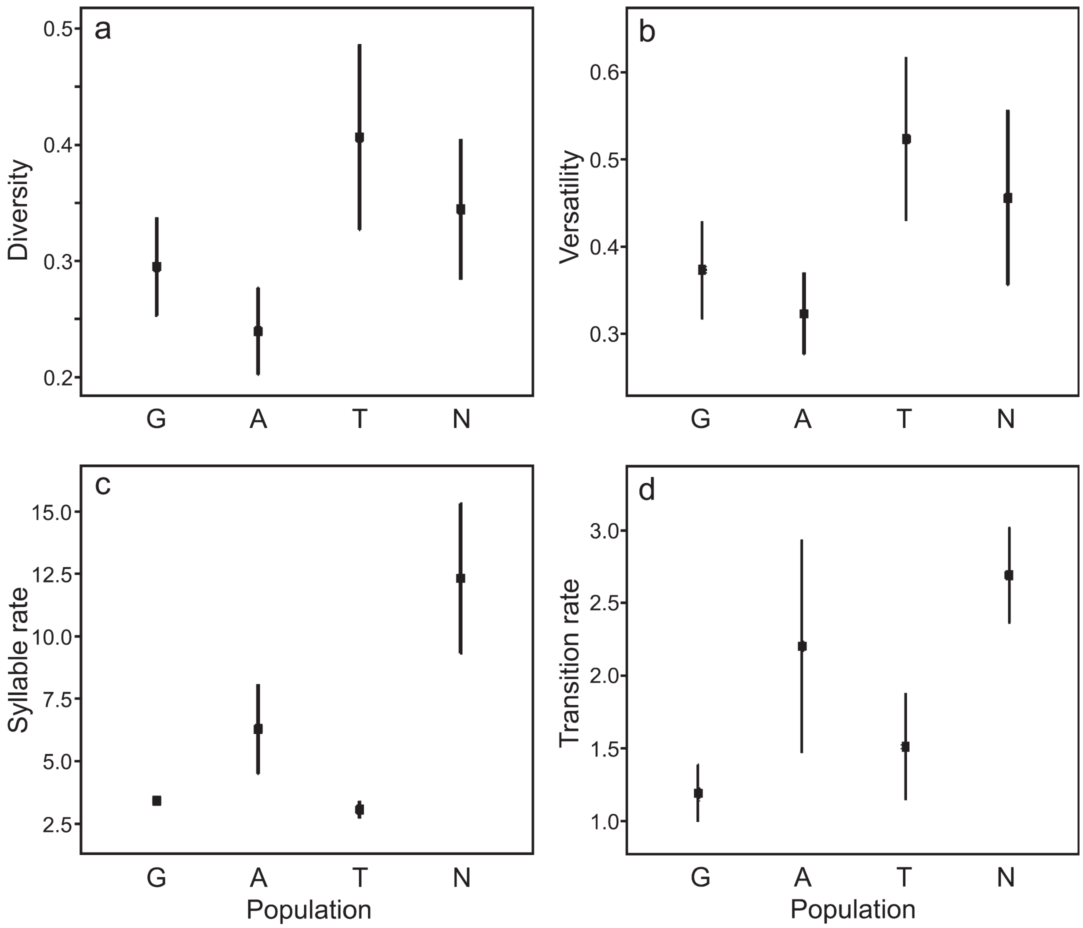

Fig. 4. Differences in structural characteristics among populations. Diversity (95% CI); versatility (95% CI); syllable rate (95% CI); transition rate (95% CI). G = Giant Mountains, A = Abisko, T = Třeboň, N = Noteć (G, A = *Luscinia s. svecica*, T, N = *Luscinia s. cyanecula*).

tended to produce slightly longer pause lengths than did males from the other populations. Comparisons of temporal parameters showed clear differences between the two Czech populations, but not between subspecies.

3.4. Structural characteristics, and neighbour effect

The studied populations differed in the structural song characteristics of diversity and versatility (Fig. 4a–b). As these variables were correlated (Spearman's $r = 0.873$, $P = 0.01$, $N = 50$) and both reflect song complexity, only diversity differences among populations were considered ($F_{3,46} = 7.56$, $P < 0.001$). Males of both *cyanecula* populations produced more diverse songs than did males from the two *svecica* populations. Bonferroni *post hoc* tests revealed that in terms of song diversity the Abisko population significantly differed from the populations of Třeboň and Noteć ($P = 0.037$ and $P < 0.001$, respectively). Moreover, the population of the Giant Mountains differed from that of Třeboň ($P = 0.023$), but not from that of Noteć.

The number of transitions per song did not significantly vary among populations ($\chi^2 = 3.51$, df = 3, $P = 0.32$), although populations differed in the number of syllables produced per song ($F_{3,\ 46} = 6.33$, $P = 0.001$). The Třeboň population significantly differed from the populations of the Giant Mountain and Abisko (Bonferroni *post hoc* test: P

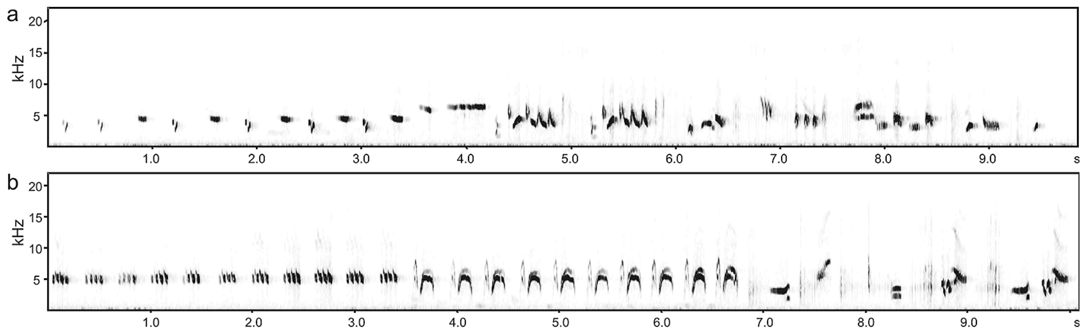

Fig. 5. Examples of Bluethroat songs. (a) A diverse or versatile song of *L. s. cyanecula*. (b) A song of *L. s. svecica* rich in repetitions of a particular syllable type.

= 0.015 and $P = 0.001$, respectively). Noteć males tended to produce slightly fewer syllables per song. Males of *svecica* used more repetitions of one syllable type, with fewer switches among different syllable types, in their songs, which resulted in their songs having lower diversity (Fig. 5).

Only the Noteć population differed from the other populations in syllable rate ($\chi^2 = 36.132$, df = 3, $P = 0.05$) and transition rate ($\chi^2 = 19.404$, df = 3, $P = 0.05$), indicating that these differences appeared at the population level but were inconsistent at the subspecies level (Fig. 4c–d). Repertoire sizes, as estimated by visual examination of sonograms, did not differ significantly between the Czech populations ($U = 71.5$, $n_1 = 13$, $n_2 = 12$, $P = 0.723$).

The density of neighbouring males differed significantly between the two Czech populations ($U = 22$, $n_1 = 13$, $n_2 = 12$, $P < 0.025$). The number of neighbours per each recorded male was lower in the Giant Mountains than in Třeboň.

4. Discussion

Songs of Bluethroat males, obtained from four populations of two subspecies representing genetically distant groups of the subspecies complex, significantly differed in frequency parameters but not in temporal parameters. The results from two populations of each subspecies indicate that *cyanecula* males produce songs of higher frequencies than do *svecica* males. These results are consistent with the assumption that frequency parameters are song features with stronger influence of genetic background (Forstmeier *et al.* 2009), and are therefore more likely to be similar at the subspecies level. On the other hand, song features more related to behaviour – such as temporal patterns of singing, or song syntax – should be more flexible and therefore may differ between populations of the same subspecies (Atwood *et al.* 1991). The Giant Mountains population was established only recently, and has apparently originated from Scandinavia and/or north-western Russia (Johnsen *et al.* 2006). It is therefore not surprising that songs of the two studied *svecica* populations did not significantly differ in frequency parameters, although the songs of *cyanecula* males were apparently higher in frequency.

We assumed that Bluethroats would adjust their song frequencies according to the habitat in which the song is being transmitted. Songs with low frequencies and low frequency modulations are often performed in habitats with complex and dense vegetation structure, whereas high frequencies, high frequency modulations and broad bandwidths may be prevalent in open habitats (the acoustic adaptation hypothesis; Morton 1975). *Cyanecula* males often sing perched in the middle of a reed stalk (L. Turčoková, pers. obs.), and thus the surrounding reed vegetation might partially degrade song characteristics.

Svecica males, in contrast, are usually perched in the upper parts of dwarf pine or spruce trees while singing. One might, therefore, expect lower frequencies in the songs of *cyanecula* males; however, the present results did not support this idea. Bluethroats often sing in flight (e.g., Merilä & Sorjonen 1994), so the influence of vegetation on song structure might be negligible. The breeding habitat structure, particularly vegetation cover, may thus only play a minor role in the adjustment of Bluethroat song.

Song features are influenced by body size (Ryan & Brenowitz 1985, Tubaro & Mahler 1998, Kipper *et al.* 2006). A large vocal organ is able to produce sounds with lower frequency and relay signals better (Bradbury & Vehrencamp 1998). Body size is often correlated with vocal tract size (Fitch 1999), which influences acoustic signals (Daley & Goller 2004). Our results that males of *L. s. svecica* sang songs of lower frequencies support this hypothesis: *svecica* males from the Giant Mountains were significantly larger than those of *cyanecula* from the Czech lowlands, the same was true also for males from Abisko, located in the arctic tundra (V. Pavel, unpubl. data). These observations corroborate the measurements given in Cramp (1988), showing that individuals of *svecica* tend to be slightly larger and heavier than those of *cyanecula*. Moreover, analyses of song and body parameters of *svecica* males in the Giant Mountains revealed a negative correlation between body mass and frequency characteristics within a population (Fig. 2). We therefore suggest that the larger size of *svecica* males is responsible for frequency differences between subspecies.

For temporal parameters, there was no such trend in subspecies divergence, and the variation was rather observed at the population level. Significant differences in temporal patterns were only detected between the Czech populations: *svecica* males from the Giant Mountains tended to produce longer songs with longer pauses, which resulted in a lower song rate. The *cyanecula* population of Třeboň apparently had shorter song duration.

The most likely explanation for these differences is the improvement of communication over long distances. Thrush nightingales *(Luscinia luscinia)* increase song length and decrease pause length to enhance the receiver's detection ability (Sorjonen 1986b). Due to the lower density of males in the mountains, larger breeding territories can be occupied (L. Turčoková, pers. obs.). Singing males may thus need to increase the likelihood that both males and females are able to detect the delivery of acoustic messages (Catchpole & Slater 1995) and decode them properly (Krams 2001). However, this may also increase the predation risk (Hale 2004), as many predators use acoustic cues to detect prey (Møller *et al.* 2006). Taller or denser habitat structure generally increases visual obstructions for birds (Butler & Gillings 2004), and may increase predation risk (Cresswell 1994). Predation risk might be higher in dense reed vegetation where Bluethroats may consequently sing very short songs to avoid detection by predators. On the contrary, Bluethroat males at high altitudes in the Giant Mountains are unlikely to increase their predation risk by singing long songs because the only predator that can detect them acoustically in the area is the Peregrine Falcon (*Falco peregrinus*), which occurs at a low density there (1–3 breeding pairs across the mountain range, L. Turčoková, unpubl. data).

In contrast to temporal patterns, the song structure parameters significantly varied among populations and indicates differences between the two subspecies. The songs differed in syntax, with a lower number of repetitions in *cyanecula* songs, resulting in higher diversity and versatility. As *cyanecula* are smaller than *svecica*, these more diverse songs could be a way to save energy: frequent song switching requires different muscles, and thus lower exhaustion may allow a higher rate to be maintained (the anti-exhaustion hypothesis; Lambrechts & Dohnt 1988). *Svecica* males used more repetitions of one syllable type with fewer switches among different syllable types in their songs, which can improve the transmission of information over long distances. Repetition and redundancy are important cues in the transmission of acoustic signals over long distances (Kroodsma & Miller 1982).

Song diversity can be advantageous in minimizing receiver habituation (Hartshorne 1956) or in bypassing competing noise (Schleidt 1973). *Cyanecula* males produced more diverse songs in populations with high density of both conspecifics and other songbirds, where ambient noise is large and males have to compete for acoustic niches.

Bluethroats are a strongly imitative species with large repertoires (Cramp 1988). As the breeding localities of *cyanecula* males had dense bird communities, a larger repertoire size for these males was predicted. However, the repertoire size did not significantly differ between the Czech populations. A possible explanation for this similarity is that Bluethroat males imitate songs from not only the breeding areas but also from wintering and stopover areas (Cramp 1988). Although males produce many syllable types, repertoire size might not be a reliable signal of male quality in the Bluethroat. Selection pressure could lead to song-sharing among neighbours (Beecher 2000, Grießmann 2002) rather than to an enlargement of repertoire size through female choice (Lampe & Saetre 1995, Hasselquist *et al.* 1996). Indeed, Bluethroat males learn from each another (Cramp 1988), which predicts syllable sharing among neighbouring males. Recent studies have introduced the hypothesis that repertoire size may be a byproduct of social interactions (Byers & Krooodsma 2009), which might apply to Bluethroats.

The present results demonstrate differences in the song characteristics between two Bluethroat subspecies. Together with other differences, such as size, colouration and habitat, these differences in song features might be used in subspecies recognition and influence the speciation process. In various species, females preferentially mate with males sharing the same dialect (Clayton 1990, Vaneechoutte 1997, Freeberg *et al.* 1999, Riebel 2000). As populations or subspecies become more and more isolated, individuals of different origin might become unable to recognize each other as potential sex partners. This situation may reduce gene flow between populations and initiate speciation. Therefore, future studies to experimentally test the Bluethroats ability for subspecies recognition are the essential next step.

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Sinirinnan alalajien laulutavan eriytyminen

Lintujen sopeutuessa muuttuviin elollisen ja elottoman ympäristön oloihin niiden ääntelyn (akustisten signaalien) osatekijät muuttuvat valintapaineiden mukaan siten, että yksilöiden välinen kommunikointi on mahdollisimman tehokasta. Tällaiset laulun osasten muutokset voivat johtaa akustisiin, populaatioiden välisiin eroihin lajin sisällä.

Tutkimme laulun eroja neljällä sinirinnan populaatiolla, jotka edustivat kahta alalajia: *Luscinia s. svecica* ja *L. s. cyanecula*. Ensin mainitun koiraat, jotka asuttavat tundraympäristöä, lauloivat vähemmän vaihtelevasti ja matalataajuisemmin kuin alalajin *cyanecula* koiraat, jotka asuttavat useampia ympäristötyyppejä. Odotuksien vastaisesti repertuaarien laajuus ei eronnut merkitsevästi alalajien välillä. Yksilöt ilmeisesti sopeuttivat laulun taajuutta ja äänteellistä rakennetta (vaihtelu, muuntuvuus) ”akustisen lokeronsa” mukaan. Laulun aikamuuttujat (laulun ja taukojen pituus ja laulunopeus) erosivat merkitsevästi populaatioiden mutteivät alalajien välillä. Lauluerot voivat olla tärkeitä alalajien tunnistamisessa ja siten ylläpitää alalajien eroja ja jopa vaikuttaa lajiutumiseen.

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