The song structure of the Siberian Blue Robin *Luscinia* [Larvivora] cyane and a comparison with related species

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**Abstract** We studied the song syntax of the Siberian Blue Robin *Luscinia cyane*, a small insectivorous passerine of the taiga forests of Siberia and the Far East. Males have repertoires of 7 to 14 (mean 10.9±2.3) song types. A single song typically consists of a short trill comprised of from three to six identical syllables, each of two to three notes; sometimes the trill is preceded by a short single note. The most complex songs contain as many as five or six different trills and single notes. The song of the Siberian Blue Robin most closely resembles that of the Indian Blue Robin *L. brunnea*. The individual repertoires of Siberian Blue Robin, Common Nightingale *L. megarhynchos* and Thrush Nightingale *L. luscinia* contain groups of mutually associated song types that are sung usually one after another. The Siberian Blue Robin and the Common Nightingale perform them in a varying sequence, while Thrush Nightingale predominantly uses a fixed sequence of song types. The distinctions between the song syntax of *Larvivora* spp. and *Luscinia* spp. are discussed. The individual songs of *Luscinia* spp. are much more complex and are performed with less prolonged pauses than those of *Larvivora* spp.

**Key words** Avian song, *Larvivora cyane*, Syntax

The study of avian vocalisations significantly contributes to our understanding of evolutionary biology and taxonomy. Although advances in taxonomic research are associated mostly with molecular genetics, comparative bioacoustic studies can also shed light on the evolutionary relationships among species and clarify the taxonomic structure of a selected group (Payne 1986; Alström & Ranft 2003).

The songs of species in the genus *Luscinia* have attracted considerable attention due to their great variety and their complex structure. As many as 18 species are included in the genus *Luscinia sensu lato*, but the taxonomic position and composition of this genus still remain subjects of debate (Sangster et al. 2010). Only a few species have been studied in detail, from the perspective of bioacoustics; among them are: Common Nightingale *L. megarhynchos* (Hultsch & Todt 1989; Sprau & Mundry 2010; Weiss et al. 2014), Thrush Nightingale *L. luscinia* (Sorjonen 1987; Naguib & Kolb 1992, Grießmann & Naguib 2002; Ivanitskii et al. 2013; Marova et al. 2015) and Bluethroat *L. svecica* (Naguib & Kolb 1992; Turčoková et al. 2010). More recently, Alström et al. (2013), and Song et al. (2014) have addressed briefly the songs of Blackthroat *Luscinia obscura* and Firethroat *L. pectardens*.

The song of the Siberian Blue Robin (a small taiga forest passerine that ranges from West Siberia eastward to the Japanese islands), has never before been the subject of special research. Previously, only a brief description of its song and data on its breeding ecology and territorial behavior have been published (Tamura & Ueda 2001a, b). The aim of our research was to describe the Siberian Blue Robin’s song in great detail and to conduct a comparison among different species of robins and nightingales, including the Indian Blue Robin *L. brunnea*, which has recently been recognized as the closest relative of the Siberian Blue Robin (Sangster et al. 2010).
MATERIALS AND METHODS

Our recordings were made with a Marantz PMD-660 recorder and a Sennheiser-IU 66 microphone near Krasnoyarsk (four males in “Stolby” State Reserve in 2009), in the Amur region (three males in “Kchingansky” Reserve in 2013), in the Tomsk Region (three males in 2014) and near Nachodka (seven males in 2004–2005). No playback was used, and each male was recorded only once. Forty-six to 89 songs were recorded per male. The breeding status of most males was not controlled because of their extreme caution and timidity. We used also the recording of three males made in Kedrovaya Pad Reserve by BN. Veprintsev (in Veprintsev’s Phono-logue numbers and recordists: XC96490 D. Marques; XC103690 D. Wagner; XC110069, XC111185 and XC110837 F. Lambert; XC20191 N. Athanas; XC81053 Y. D. Li).

Song visualization and measurement was done using Syrinx 2.5s (JM. Burt: http://syrinxpc.com) with 512 FFT and Blackman window. For each song we measured: 1) maximum frequency (kHz); 2) minimum frequency (kHz); 3) frequency range (kHz); 4) song length (seconds); 5) pause length (length of the pause following the song; seconds); 6) total number of syllables; 7) number of syllable types. The mean values are presented below with standard deviations.

Data were processed in PAST v.2.15b (Hammer et al. 2001). To verify the differences between groups we ran: two-tailed non-parametric MANOVA tests with 9,999 permutations, Bray-Curtis measures for intra-group and between group distances, and Bonferroni corrections for multiple comparisons (Anderson 2001).

For the syntax analysis we used four vocal sessions each for Siberian Blue Robin and Thrush Nightingale. First, a catalogue of song types was created for each male; then the complete sequence of song types was determined. We used two variables (indices) to describe the sequence of the different song types: a linearity index, and a modified linearity index. The linearity index (index A) is the ratio of the number of song types in the repertoire to the number of switches between different types of song. If the vocal session is represented as a transition matrix, the linearity index is calculated by dividing the number of rows by the number of cells filled with non-zero content (Scharff & Nottebohm 1991). The second index (index B), a modified version of index A, is the ratio of the total number of the most frequent transitions calculated for each song type to the total number of transitions between all types of songs in the vocal session. The limits and variation of both of these indices are the same: from 1 (completely determinate sequence; in each matrix row all transitions are concentrated in one cell) to a very small value (random sequence; transitions are distributed across many cells in the row).

RESULTS

The Siberian Blue Robin’s song is a short, loud trill clearly separated by pauses. Each subsequent song normally belongs to a type different from the previous one (immediate variety). Typical songs contain three to five identical syllables, each consisting of two or three notes (Fig. 1; 2, 10, 11, 12). In some songs, trills are preceded by single tonal introductory notes (Fig. 1; 3, 4, 13). More complex songs may contain up to five or six different vocal components (trills and single notes) (Fig. 1; 2, 10, 11, 12). The repertoire of individual males includes 7–14 song types (average 10.9±2.3). A total of 134 song types was identified, 57 in Siberia and 88 in the Far East, with only 11 present in both groups.

The frequency band of singing is wide (1.7 to 8.8 kHz), but individual songs typically occupy a more limited range (Fig 1). One male may present different song types in a completely different (non-overlapping) range. The very slow pace of the singing is a very distinctive feature. The pauses between songs are about ten times longer than the songs themselves (Table 1) and are usually filled with short (~ 30–40 ms) sounds that lie in the narrow range (~ 250–300 Hz) at a frequency of 4.9±0.18 kHz (Fig. 1; 8–11). The duration of pauses between these sounds is about 300 ms. The periodicity of sound emission remains highly uniform during the whole singing. These quiet sounds are characteristic of the Siberian Blue Robin’s song, as previously described by Tamura and Ueda (2001a). The differences between the basic parameters of the songs of Siberian Blue Robin and Indian.
Blue Robin are highly significant (P<0.001) (see Table 1).

The vocal sessions of four male Siberian Blue Robin and four male Thrush Nightingale were “sequenced” (see Fig. 2), with filling and framing designating repeated clusters of song types. Some clusters were performed more frequently than expected by chance alone. Consider, for example,
the combination of song types 92 and 93 in male B. Initially we assumed that they were performed independently. Given the number of times each was performed (nine times for song type 92 and eight times for song type 93) and the total number of songs in this vocal session (56), the expected probability of their execution one after another in any order, is \( P = 9/56 \times 8/56 = 0.02 \). This means that one should expect the appearance of only two combinations of song types 92 and 93 among 100 randomly selected paired executions from the repertoire of this male. In fact, there were six combinations of song types 92 and 93 among 55 paired combinations presented in this vocal session. Thus, the observed frequency of sequential execution of song types 92 and 93 was 0.11. According to Fisher’s exact test, the difference between observed and expected frequencies is significant (\( P = 0.02 \)). More complex clusters were also repeated. For example, the vocal session of male D contained three combinations of song types 9, 36, 42 and 44. Each time these song types were performed immediately one after another, albeit in a variable

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**Table 1.** Basic parameters of the songs of Siberian Blue Robin and Indian Blue Robin.

<table>
<thead>
<tr>
<th>Song Parameters</th>
<th><em>L. cyane</em></th>
<th>Limits</th>
<th><em>L. brunnea</em></th>
<th>Limits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum frequency, kHz</td>
<td>6.2±1.4</td>
<td>3.8–8.8</td>
<td>7.4±0.2</td>
<td>6.7–7.6</td>
</tr>
<tr>
<td>Minimum frequency, kHz</td>
<td>3.0±0.8</td>
<td>1.6–5.2</td>
<td>2.9±0.6</td>
<td>2.0–4.6</td>
</tr>
<tr>
<td>Frequency range, kHz</td>
<td>3.1±0.9</td>
<td>1.6–5.4</td>
<td>4.5±0.6</td>
<td>2.9–5.3</td>
</tr>
<tr>
<td>Song length, s</td>
<td>1.0±1.1</td>
<td>0.7–1.4</td>
<td>1.1±0.1</td>
<td>0.9–1.3</td>
</tr>
<tr>
<td>Pauses between songs, s</td>
<td>11.2±3.0</td>
<td>7.8–15.9</td>
<td>18.4±10.9</td>
<td>5.0–33.1</td>
</tr>
<tr>
<td>Number of syllables</td>
<td>6.5±2.8</td>
<td>2.0–17.0</td>
<td>6.4±1.7</td>
<td>4.0–10.0</td>
</tr>
<tr>
<td>Number of syllable types</td>
<td>1.6±0.6</td>
<td>1.0–4.0</td>
<td>2.4±0.7</td>
<td>1.0–4.0</td>
</tr>
</tbody>
</table>

**Fig. 2.** Sequences of different song types of four male Siberian Blue Robins (A, B, E, F) and four male Thrush Nightingales (C, D, G, H). Numbers indicate different song types. The same numbers for different males represent different songs type. Shaded and framed song types indicate repeating clusters (sequences of song types).
sequence. The expected probability of such events is about 1 out of 10,000 cases, a value that is negligibly small compared with the observed frequency of this combination.

Similar syntax patterns are obvious in the song syntax of all of the Siberian Blue Robin and Thrush Nightingale males studied. Apparently, the production of different song types is not a purely random process. Some song types are mutually associated and are usually performed together as a sequence or cluster. In the Siberian Blue Robin, the order of their performance varies. In one case, the sequence may be performed as A → B → C, in another as B → A → C, or, alternatively, as C → B → A. The available data suggest that one combination may include at least four different song types. Longer recordings are needed to achieve a more complete and detailed picture.

Unlike the Siberian Blue Robin, the Thrush Nightingale uses linear syntax. It sings individual songs, belonging to a given cluster, in a fixed order of (Figs. 2 C & 2 F). In the Thrush Nightingale, such song types are usually executed one after another in a strict sequence according to a fixed program that may include up to six song types. In most cases, sequence execution begins with the first type of song, but it may end after any song in the sequence. The order of execution of the various sequences, is also fixed (Ivanitskii et al. 2013).

The differences in the syntactic organization of the songs of Siberian Blue Robin and Thrush Nightingale are clearly identifiable in the positions of males against the two axes corresponding to the linearity indices (Fig. 3). The 75% ellipses encompassing the points representing these two species (each point corresponds to one male) do not overlap. The interspecific differences between the index values is statistically significant despite the very limited sample size (P=0.028; non parametric MANOVA with permutations).

**DISCUSSION**

The size of the individual repertoire of the Siberian Blue Robin is very similar to that of the Thrush Nightingale (Sorjonen 1987; Ivanitskii et al. 2013), whereas the repertoire of the Common Nightingale is much more extensive, with one male performing as many as 146–280 song types (Hultsch & Todt 1989; Sprau & Mundry 2010).

Despite the differences in the repertoire size the song syntax of Siberian Blue Robin and Common Nightingale shows similar traits while the Thrush Nightingale stands apart from them. Groups of mutually associated song types, which are usually performed one after another (song clusters), are present in the songs of all three species. However, the songs of these species have certain syntactic differences, mainly due to their adherence to predominantly linear (unidirectional) or combinatory (multidirectional) syntax.

Syntactic organization in the song of the Common Nightingale has been investigated in detail (Hultsch & Todt 1989; Weiss et al. 2014). All of the song types composing the extensive repertoire of a single male are stored in its memory in short clusters (song packages). One package contains from two to seven (average four) song types. Songs belonging to one package are performed together more often than with other songs, but the order of their presentation, and the number of songs performed varies from case to case. Thus, the composition of a vocal session by a Common Nightingale is based on predominantly combinatory syntax, i.e. individual songs in a package are combined relatively freely. It seems that the songs of Siberian Blue Robin and Common Nightingale are by-and-large similar with regard to their syntactic organization. Unlike these two species
the Thrush Nightingale mainly uses linear syntax, i.e. individual songs performed in a fixed order (Figs. 2 C & 2 F).

Recent molecular research has indicated that the genus *Luscinia sensu latu* is polyphyletic, thus while assigning Siberian Blue Robin to the genus *Larvivora* along with with *L. akahige, L. brunnea, L. komadori, L. ruficeps*, and *L. sibilans* is strongly advocated (Seki 2006; Sangster et al. 2010), while Thrush Nightingale, Common Nightingale, Bluethroat, and probably also *L. [Irania] gutturalis* are to be included in the genus *Luscinia* sensu stricto.

The song of the Siberian Blue Robin bears a very strong similarity to that of the Indian Blue Robin (Fig. 1). In both species, one song usually includes three to six identical syllables, consisting of two to three notes each. Sometimes the song is preceded by a short monosyllabic note. In particular, each individual song of both species is preceded by a sequence of short, quiet notes given in a very uniform manner. Both of these species typically sing at a very slow pace with prolonged pauses between song phrases. There is a slight difference between them, but only in the frequency parameters. The Indian Blue Robin sings in a frequency range that is somewhat narrower and apparently more constant (2.4–7.2 kHz) than that of the Siberian Blue Robin (1.6–8.9 kHz). In general, their basic song structure is surprisingly similar given their considerable difference in external appearance (plumage coloration). Complete geographical isolation could be one reason for the reduced divergence in their songs. In contrast, the songs of the Siberian Blue Robin and the Rufous-tailed Robin, the geographical ranges of which overlap extensively, are much more different and they can be heard singing side by side in the same habitat.

In terms of bioacoustics, the most important distinction between the genera *Larvivora* and *Luscinia* is that the individual songs of the latter have a much more complex structure. The typical song of *Luscinia* consists of three to six trills (phrases) whereas the typical *Larvivora* song frequently contains only one trill (phrase) preceded by one or two introductory notes. A further difference concerns the overall rhythm of singing; successive song phrases of *Larvivora* are separated by pauses, which are much longer than the song phrases. In contrast, the pauses between song pauses in *Luscinia* are generally shorter than their songs. For example, Thrush Nightingale songs are 1.5–14.0 s (average 6.2±2.8 s) long, while the pauses between their songs range from 0.2 to 7.3 s (average 2.4±0.7 s). When singing at maximum speed, these pauses are reduced to just 0.12–0.15 s. Such short pauses, are comparable to the pauses between syllables within a song (on average 0.130±0.05 s); however, the structure of individual song types remains well preserved (Ivanitskii et al. 2013).

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