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Distinct patterns of geographic variation for different song components in Daurian Redstarts Phoenicurus auroreus

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ABSTRACT

Capsule: Components of Daurian Redstart Phoenicurus auroreus song have evolved along independent trajectories and show a mix of clinal and dialect patterns of geographic variation.
Aim: To investigate multiple structural components of song in Daurian Redstarts Phoenicurus auroreus as they varied among five locations across South Korea. To test whether different components of the same signal can evolve along independent trajectories, or else are constrained to evolve in correlated fashion.
Method: Two distinct song components were investigated: the introductory whistle and the complex syllable. For both segments, we made both qualitative and quantitative comparisons of similarity among individuals both within and among populations.
Result: Patterns of geographic variation differed substantially between the two song segment types. Introductory whistles varied widely both within and among individuals, and were distributed across space in a mosaic pattern. Complex syllable parts showed high within-individual similarity and a distinctly clinal pattern of geographic variation, with the exception of a distinct dialect in one population isolated by a high-elevation mountain range.
Conclusion: The results suggest that different components of Daurian Redstart songs have evolved along independent trajectories; that specific song components may show a mix of clinal and dialect patterns of geographic variation; and that different song components might simultaneously transmit distinct patterns of information about individual, dialect or species identity.

Animal mating signals often include multiple components within a given sensory modality, such as colour and geometry in visual signals (White 2017). Theory predicts that distinct signal components can, in some circumstances, evolve along independent trajectories, especially if they are decoupled mechanistically and serve distinct functions (Hebets & Papaj 2005). Support for this theory might be garnered in a number of ways, including one that so far has been mostly overlooked; distinct patterns of geographic variation for different signal components. Operationally, geographic variation can be quantified as degrees of structural similarity across signal types, within populations and across populations (Marler & Tamura 1962, Mundinger 1982). One taxon for which patterns of geographic variation in signals have been studied quite extensively is songbirds (Passeriformes: Oscines); in this group, vocal geographic variation typically results from cultural evolution, as birds learn their songs through vocal imitation, with different traditions being retained in different populations. As with genetic evolution, resulting variations in song caused by cultural evolution can impose strong driving forces for divergence within and among species. Much interest in these processes has focused on how they might facilitate early stages of speciation (Slabbekoorn & Smith 2002, Wilkins et al. 2013); geographical analyses might also address questions about the evolution of distinct components in complex signals.

Overall, structural analyses of birdsong have identified three main patterns in geographic acoustic variation: random and clinal patterns, and dialects. Random variation has no discernible pattern, clinal variation shows gradual changes of song variants over distance, and dialects form well-defined boundaries with different song variants between neighbouring populations. Describing these patterns in natural systems can provide insight into the process that drives song divergence, and also the potential for reproductive isolation and speciation (Podos & Warren 2007). Clinal patterns in bird songs have been reported in quite a few species, especially those with multiple
songs in their repertoires. In such species, syllable and song type sharing among males is seen to decrease with increasing distance, as in Great Tits *Parus major* (Falls *et al*. 1982, McGregor & Krebs 1982), Lincoln’s Sparrows *Melospiza lincolni* (Cicero & Benowitz-Fredericks 2000), Savannah Sparrows *Passerculus sandwichensis* (Sung & Handford 2006) and Hermit Warblers *Setophaga occidentalis* (Janes *et al*. 2017). By contrast, song dialects have been described mainly in species with small or single song repertoires, as in Corn Buntings *Emberiza calandra* (McGregor 1980), Rufous-collared Sparrows *Zonotrichia capensis* (Handford 1988), Smith’s Longspurs *Calcarius pictus* (Briskie 1999), Orange-tufted Sunbirds *Nectarinia osea* (Leader *et al*. 2000) and Common Chaffinches *Fringilla coelebs* (Astakhova 2012).

Much of the published discussion on song geographic variation has focused on dialects, and two classes of hypotheses that might explain their origins (Podos & Warren 2007, Irwin *et al*. 2008). Non-adaptive or stochastic hypotheses invoke neutral process such as historical or random events, including cultural drift, mutation (copying errors), immigration, and song learning in isolated populations. By contrast, adaptive or deterministic hypotheses presume an influence of natural or sexual selection, associated with factors such as female preferences, ecological adaptation, urbanization, and habitat differences. The latter set of hypotheses assume social and local benefits through correct song learning among neighbouring individuals, and that song variation will co-vary with ecological and sexual traits, or with intensity of sexual selection (Wilkins *et al*. 2013). By contrast, relatively little emphasis to date has been placed on clines.

In this paper, we offer a first description and analysis of geographic variation in multiple song components in a songbird species that is distributed widely across South Korea, the Daurian Redstart *Phoenicurus auroreus*, a common, sedentary species that lives near human settlements, parks, scrub and forest edges (Lee *et al*. 2000). The songs of the birds consist of a variable series of short, sweet, mostly descending phrases typically starting with 1–6 short clear notes, the ‘whistle’ part, followed by a scratchy trill and a wheezy jingling flourish, with some clear slurred notes, the ‘sub-syllable’ and ‘syllable’ parts (Figure 1). Each bird sings multiple song types (mean ± sd = 5.65 ± 1.05, range 3–8, JHL, unpublished data), with variations evident in both whistle and syllable parts. There have been no studies on the song learning process for this species. As described in a prior study on this species in China (Huang *et al*. 2012), whistles in the stereotyped part of the song are individual-specific, whereas the syllable part is more variable, consisting largely of additions or deletions of individual notes. Thus, Huang *et al*. (2012) suggested that individual identity is possibly encoded in whistles but not in syllables. However, pilot work on this species across South Korea found that the whistle variations among individuals were less than expected in the previous study and that geographic variations appeared in both whistle and syllable parts of the song.

Here we conducted distinct analyses on the two song parts, whistles and syllables, which, given our pilot work, appear to be distinct in their patterns of variation. We characterized geographic song variations among males from five sites at three levels: within individuals, within populations, and among populations at an intermediate spatial scale (35–350 km). Our analyses focused on degrees of similarity among different song pairs, with similarity defined by the degree which two songs share basic acoustic units. Following Huang *et al*. (2012), generally speaking, we expected to find the greatest variation in songs among populations and the least

FIGURE 1. Spectrogram of a typical Daurian Redstart song showing song structure and codes of whistle and syllable types.
variation to occur within individuals. Moreover, if the geographic structure of the songs is clinal, we expected the degree of similarity among individuals’ songs to decrease over increasing geographic distances, and that neighbouring populations would be grouped closely in cluster analyses based on the pairwise similarity of song components. Finally, dialect patterns would be characterized by low within-population structural variation set against high between-population structural variation, and without any clear relationship between population distances and degrees of song dissimilarity. Thus, in this study, geographic variation in song structure at each part of whistle and syllable was investigated in populations of the Daurian Redstart in South Korea.

**Methods**

We identified five regions in the Korean Peninsula based on distributions of mountain ranges and administrative districts, as illustrated in Figure 2: Area A (Northwest site), Area B (Northeast site), Area C (Middle-west site), Area D (Middle-east site), and Area E (Southwest site). Area B was especially well separated from the other areas by high-elevation mountain ranges, and similarly Area D was particularly well separated from Areas A and C. Among study areas, average elevation gradients of males ranged from 57.3 to 310.2 m above sea level, and shortest distances between recorded males within areas ranged from 35.9 to 343.3 km (Figure 2).

Across the five areas, we recorded songs of Daurian Redstart males during the breeding season from late February to March in 2015 and 2016, mainly at or near villages and forest edges. Recordings were conducted between 30 minutes before sunrise and 11:30 hour, and between 15:00 hour and sunset. Recordings were made using a Marantz PMD660 digital recorder with a Telinga Pro 8 DAT parabolic microphone at a sampling rate of 48 kHz, following mainly roadside fences in one direction to avoid recording the same male twice. All recordings were performed by JHL. A total of 63 males were recorded for more than 10 minutes per male (sample sizes per site provided in Figure 2 legend). Song spectrograms were produced using Raven Pro 1.4 (Cornell Laboratory of Ornithology 2011), using a 512 sample Fast Fourier Transform and a Hann smoothing window, resulting in a temporal resolution of 2 ms and a frequency resolution of 15 Hz.

As noted above, Daurian Redstart songs can be subdivided into three parts: whistles, sub-syllables and syllables (Figure 1). The whistle part is composed of several notes with consistent frequency ranges and simple forms (Huang et al. 2012). Next come the sub-syllable part, which is a brief note with limited syllable types. The song then closes with the syllable part, which contains numerous notes with varying frequency ranges and complex forms. In a pilot study, we found that the syllable part of songs showed the most variation, whereas the whistle part was least variable based on the cumulative number of types per bird.

**Figure 2.** Map of the Korean Peninsula and recording sites in this study: Northwest site (Youngseo districts; Area A, 12 males), Northeast site (Youngdong districts; Area B, 14 males), Middle-west site (Chungcheong area; Area C, 10 males), Middle-east site (North Gyeongsang area; Area D, 16 males), Southwest site (Jeolla area; Area E, 11 males). (a) Percent distribution of whistle types in each geographic population of Daurian Redstart; (b) representative whistle types.
sampled. This difference suggested that these two song components may show different patterns of geographical variation, and perhaps serve different functions. Thus, for the remainder of this study, we focused on the whistle and syllable parts.

Our total sample size across the 63 males was 1760 songs. Whistle and syllable types were recognized and catalogued by inspection based on the temporal, amplitude and frequency structure of notes; our classification efforts were consistent with blind classifications made by other scientists (Lee 2017). To examine the frequency of use for each whistle type, we selected a random subsample of 1000 high-quality songs: 10 males from each of the five study areas, 20 songs per male. To investigate intra- and inter-individual whistle and syllable similarity within and among populations, we randomly selected a subsample of 400 songs: four males from each of the five study areas, 20 songs per male. Whistles and syllables of each song were coded as sequences of distinct note types. For the whistle part, we quantified similarity between all possible pairs of songs between males within and among populations using the ‘simple matching’ coefficient (SM; Sokal & Michener 1958), which is calculated as the number of matches divided by the total number of comparisons. SM has a value between 0 (complete dissimilarity) and 1 (complete match). For syllables, we quantified similarity between all possible song pairs within males, between males within populations, and between males among populations using an adjusted Jaccard’s coefficient, Sj(adj), as in Tracy & Baker (1999), which is

\[ S_j(\text{adj}) = a / [(a + b + c) - s] \]

where \(a\) is the number of syllables shared between any two songs; \(b\) is the number of syllables unique in one song; \(c\) is the number of syllables unique in the other song; and \(s\) is the difference in the number of syllables between the two songs. Sj(adj) has a value between 0 (completely different) and 1 (completely identical).

We next quantified for each population the frequency of whistle types and syllable similarity (average Sj(adj) values), and then assessed geographic relationships among populations. Toward this end, we performed hierarchical cluster analysis, constructing dendrograms using between-groups linkages, based on squared Euclidean distances as the similarity measure. Nearest neighbour and furthest neighbour techniques produce minimum and maximum clusters, so dendrograms were compared to assess the stability of similarity clusters. In addition, we performed Mantel tests (Mantel 1967) to evaluate the effect of geographic distances on between-male song similarity. For these tests, we generated each a whistle and a syllable similarity matrix based on pairwise comparisons of individual males among populations, and a geographic distance matrix by measuring straight-line distances on the map. The two symmetric matrixes produced 10 000 permutations for randomization distributions. Normality assumptions of the data were tested and met (one-sample Kolmogorov-Smirnov test, \(P > 0.05\)). We used one-way analysis of variance (ANOVA) to analyse the degree of similarity within populations and between populations using SPSS Statistics software package (v.21, IBM Corporation). The critical value of \(\alpha = 0.05\) was used to test the significance of the results. Numerical data are presented as mean ± sd.

**Results**

**Whistle type usage**

A total of 14 whistle types was identified in our sample; the distribution of whistle types in our 1000 song sample is summarized in Table 1. For each population, between 10 and 12 whistle types were identified, with an average of 6.61 whistle types per 20 songs of a male and average of 3.17 notes per song in the whistle part. We found that each population used whistle types at different frequencies, and that the dominant and subdominant types varied broadly by site, except for between populations C and E (dominant type XI), and between populations D and E (subdominant type IV). The two most common whistle types (type XI and IV) together appeared in 39% of our sample. The simple matching coefficients for whistle use (SM, based on

<table>
<thead>
<tr>
<th>Locations</th>
<th>Number of birds</th>
<th>Number of detected whistle types</th>
<th>Mean whistle types/ male (20 songs)</th>
<th>Proportion of song with dominant whistle type/10 males (200 songs)</th>
<th>Proportion of song with subdominant whistle type/10 males (200 songs)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>10</td>
<td>11</td>
<td>6.69</td>
<td>0.19 (type III)</td>
<td>0.16 (type I)</td>
</tr>
<tr>
<td>B</td>
<td>10</td>
<td>12</td>
<td>6.25</td>
<td>0.27 (type IV)</td>
<td>0.19 (type XI)</td>
</tr>
<tr>
<td>C</td>
<td>10</td>
<td>11</td>
<td>6.58</td>
<td>0.27 (type XI)</td>
<td>0.16 (type III)</td>
</tr>
<tr>
<td>D</td>
<td>10</td>
<td>10</td>
<td>6.24</td>
<td>0.33 (type XIII)</td>
<td>0.19 (type IV)</td>
</tr>
<tr>
<td>E</td>
<td>10</td>
<td>12</td>
<td>7.31</td>
<td>0.34 (type XI)</td>
<td>0.17 (type IV)</td>
</tr>
</tbody>
</table>
matching/mismatching of types) within males was 0.25 (±0.06, range 0.16–0.59) and between males was 0.12 (±0.06, range 0.00–0.44). Looking more closely at between-male comparisons, SM coefficients within populations ranged from 0.13 to 0.21, yet between populations ranged from 0.08 to 0.17; the former coefficients were significantly greater than the latter ($F_{1,13} = 10.03$, $P = 0.007$; Table 2). The representative whistle types were shown by sites (Figure 2), and the clustering pattern based on whistle type usage varied regardless of the populations’ geographic distributions (Figure 3(A)), with two main clusters evident: for population A and D, and for populations B, C and E (note that population B was not a neighbour of populations C or E). Whistle structural similarity based on simple matching coefficients (SM) decreased slightly but significantly with geographic distance (Mantel test: $r = -3.616$, $P = 0.0003$; Figure 4).

### Table 2. Mean simple matching coefficients (SM) obtained by pair-wise between individual vs. individual comparisons within and among populations of Daurian Redstart songs.

<table>
<thead>
<tr>
<th>Area</th>
<th>Area A</th>
<th>Area B</th>
<th>Area C</th>
<th>Area D</th>
<th>Area E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area A</td>
<td>0.125</td>
<td>0.085</td>
<td>0.091</td>
<td>0.087</td>
<td>0.078</td>
</tr>
<tr>
<td>Area B</td>
<td>0.085</td>
<td>0.159</td>
<td>0.138</td>
<td>0.104</td>
<td>0.142</td>
</tr>
<tr>
<td>Area C</td>
<td>0.091</td>
<td>0.138</td>
<td>0.173</td>
<td>0.102</td>
<td>0.174</td>
</tr>
<tr>
<td>Area D</td>
<td>0.087</td>
<td>0.104</td>
<td>0.173</td>
<td>0.163</td>
<td>0.123</td>
</tr>
<tr>
<td>Area E</td>
<td>0.078</td>
<td>0.142</td>
<td>0.174</td>
<td>0.123</td>
<td>0.206</td>
</tr>
</tbody>
</table>

### Figure 3. Hierarchical clustering of the population sample showing geographic relationships among five Daurian Redstart populations based on (a) simple matching coefficients (SM) for whistle part and (b) similarity coefficients ($S_j(adj)$) for syllable part.

**Syllable similarity**

In our analysis of syllables from 400 songs, we identified a total of 2009 syllables. The distribution of syllables and syllable types is presented in Table 3. Average numbers of syllables and syllable types per song were 5.1 and 4.59, respectively. The observed syllable repertoire size within the first 20 songs from 20 males ranged from 21 to 45 (mean ± sd = 36.1 ± 5.73). Within males, syllable similarity coefficients ($S_j(adj)$) were 0.79 (±0.07, range 0.68–0.91). Summary statistics for syllable similarity between males (within- and among populations) are presented in Table 4. Syllable similarities within populations were significantly higher than among populations ($F_{1,13} = 60.902$, $P < 0.001$). Within populations, syllable similarity was lowest in population E (0.645); thus population E had the most diverse syllables, and C the least diverse syllables. Among populations, syllable similarity was lowest (0.193) between populations B and E, while highest (0.399) between A and C. A cluster dendrogram based on syllable similarity among populations (Figure 3(B)) shows strong geographic structure; the top cluster contained the neighbouring population A and C, the middle cluster joined populations D and E, and the most isolated population (B) was classified as the most distant cluster. In addition, syllable similarity among population pairs decreased markedly and significantly with geographic distance (Mantel test: $r = -6.234$, $P < 0.001$; Figure 5).

**Discussion**

We identified distinct patterns of geographic structural variation for the two song parts analysed. Before recapping those patterns, it is instructive to note that for both patterns, pairwise song similarities (based on note type sharing) were highest within-birds, intermediate across birds within populations, and lowest when comparing across populations. These patterns match general expectations in at least two ways: (1) song pairs should be most similar within birds, given that individual birds can re-use note types in successive songs; and (2) when comparing across individuals, birds in the same locations should be more likely to share notes than birds across distinct locations, given that birds in the same localities are more likely to learn their songs from common tutors. This pattern of within- versus between- population similarity suggests that geographic patterning was not random, but rather should be considered either clinal.
or dialect. We now address these possibilities for the two components (whistles and syllables) in turn.

For the opening song parts (whistles), differences among populations in whistle structure were only minor, and these differences did not covary with variation in geographic distance. The limited geographic structure of whistles is supported by two specific observations: (1) of the 14 whistle types identified in our focal sample (1000 songs of 50 males from the five populations), no types were unique in any given population; (2) the similarity of whistle types was low both within males (average SM = 0.25) and between males (average SM = 0.12). Yet, we can also state that the pattern of variation was not random. In particular, (1) dominant and subdominant whistle types (35–52%) were used differently in each population (Table 1), and (2) the within-population similarity was significantly higher than between-population similarity. The similarity of songs decreased only very gradually with increasing distance, so we are reluctant to refer to this pattern as clinal. Rather, we conclude that whistles show signatures of a weak dialect, which more precisely could be labelled as a song mosaic, meaning the geographic irregular distribution of the distinct types.

Table 3. Summary of the distribution and usage of syllable types of males within populations and among five populations in Daurian Redstart songs.

<table>
<thead>
<tr>
<th>Location</th>
<th>Number of birds (songs)</th>
<th>Mean syllable types/song</th>
<th>Mean syllables/song</th>
<th>syllables types/80 song (n)</th>
<th>unique types/locality</th>
<th>Mean syllable types/male</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>4 (20)</td>
<td>5.10</td>
<td>6.00</td>
<td>57 (480)</td>
<td>8</td>
<td>33.5</td>
</tr>
<tr>
<td>B</td>
<td>4 (20)</td>
<td>4.02</td>
<td>4.83</td>
<td>49 (376)</td>
<td>8</td>
<td>33</td>
</tr>
<tr>
<td>C</td>
<td>4 (20)</td>
<td>4.03</td>
<td>3.91</td>
<td>61 (297)</td>
<td>11</td>
<td>37.5</td>
</tr>
<tr>
<td>D</td>
<td>4 (20)</td>
<td>4.72</td>
<td>5.31</td>
<td>64 (420)</td>
<td>10</td>
<td>40.75</td>
</tr>
<tr>
<td>E</td>
<td>4 (20)</td>
<td>5.08</td>
<td>5.45</td>
<td>61 (436)</td>
<td>12</td>
<td>35.5</td>
</tr>
</tbody>
</table>

n = number of syllables in 80 song.

Table 4. Mean syllable similarity coefficients, Sj(adj), for songs within and among populations of Daurian Redstarts.

<table>
<thead>
<tr>
<th>Area A</th>
<th>Area B</th>
<th>Area C</th>
<th>Area D</th>
<th>Area E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area A</td>
<td>0.571</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area B</td>
<td>0.286</td>
<td>0.574</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area C</td>
<td>0.399</td>
<td>0.232</td>
<td>0.645</td>
<td></td>
</tr>
<tr>
<td>Area D</td>
<td>0.345</td>
<td>0.212</td>
<td>0.382</td>
<td>0.594</td>
</tr>
<tr>
<td>Area E</td>
<td>0.298</td>
<td>0.193</td>
<td>0.387</td>
<td>0.339</td>
</tr>
</tbody>
</table>

Figure 4. Whistle simple matching coefficients (SM) as a function of geographic interpopulation distance. The SM values were obtained based on pairwise comparisons of individual males within and among populations. Pairwise similarity values are seen to decrease slightly with increasing distance (Mantel test: $t = -3.616, P = 0.0003$).
One caveat here is that patterns of whistle part variation in this species might differ across larger geographic scales. In particular, whereas whistles within Korean birds are highly variable, whistles in individual birds from China were reported as being less variable, which had led Huang et al. (2012) to posit that whistles play a role in this species in individual recognition. Because of the high amount of intra-individual variation, no such opportunity to use songs for individual recognition seems available for the Korean birds. Thus the dialect variation in whistles of this species is built upon a more basal role of species-recognition. Broadening the comparison to other species, dialects have been reported in the opening sequences of the songs of at least two other species: Tree Pipits *Anthus trivialis*, which start their songs with complex syllables (Petruskova et al. 2010), and White-crowned Sparrows *Zonotrichia leucophrys nuttalli*, whose songs begin with whistles (Baker & Thompson 1985). In this latter species, playback experiments with 'hybrid' songs created by song components from adjacent dialects suggested that the whistle variations indeed facilitate dialect recognition (Thompson & Baker 1993). Another notable feature of whistles in White-crowned Sparrows is that they seem to play a key role in species recognition (Marler 1970, Soha & Marler 2000), as innate species-specific components that can direct imitative learning of subsequent song components. In other sparrow species, opening sequences do not show clear dialect variation. For example, in a study of Golden-crowned Sparrow *Zonotrichia atricapilla* songs across a macrogeographic scale (500–17 000 km), Shizuka et al. (2016) found all songs commonly contained similar introductory whistles with downward frequency modulation. Nevertheless, Golden-crowned Sparrow nestlings before song learning discriminated between conspecific and heterospecific (White-crowned Sparrow) introductory whistles (Hudson & Shizuka 2017) and both nestlings and adult males distinguished between local conspecific and local heterospecific (White-crowned Sparrow) songs (Hudson et al. 2018).

The patterns of syllable similarity we report here differ broadly from that of whistles, in three ways. First, similarity scores for syllables were comparatively higher than whistles at all levels of analysis, suggesting that the evolution and cultural transmission of syllable structure is more conserved than that of whistles. Second, syllables showed substantial variation by site, and hence a clearly structured pattern of geographic variation. This is especially evident in the higher similarity scores within-population than between-population. Third, between-population variation emerges as being clinal, given how song similarity

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**Figure 5.** Similarity values $S_{j(adj)}$ for pairs of complex syllables as a function of geographic interpopulation distance. The $S_{j(adj)}$ values were obtained based on pairwise comparisons of individual males within and among populations. Pairwise similarity values are seen to decrease with increasing distances (Mantel test: $t = -6.234, P < 0.001$).
decreases over greater distances. That is, syllable similarity between males decreased constantly with increasing distance among males, and levels of syllable similarity by hierarchical cluster analysis showed close relatedness between neighbouring populations. Clinal variation in song features has been reported in quite a few other species, including species with various levels of song repertoire sizes and sampling distances. A single-song repertoire species, the Savannah Sparrow, showed a south to northcline with more similarity between neighbouring populations ranged at 20–230 km (Sung & Hanford 2006), while a song repertoire species, the Greenish Warbler Phylloscopus trochiloides complex, showed extensive clinal patterns in song variables ranged even up to 3000 km (Irwin 2000). At finer levels of geographic sampling, clinal variation in song was also reported for the Dickcissel Spiza americana (up to 10 km; Schook et al. 2008) and the White-crowned Sparrow Zonotrichia leucophrys leucophrys (3–15.5 km; Dalisio et al. 2015). Thus, clinal patterns may be relatively common phenomena of geographic structure of songs, and our data add to these results by showing the clinal patterns of the syllable part.

As a caveat, one of the populations (B), which is isolated geographically from the others by high-elevation mountain ranges, seemed to deviate in syllable structure from the clinal pattern. This was despite the population’s relative proximity (as the crow flies) to population A. Thus a regional dialect seems to be overlaid on the broad pattern of clinal variation. This dialect perhaps resulted from limited between-site immigration and resulting cultural isolation in this population; such a process seems to have caused reduced inter-individual song variation within populations and local dialects in Mountain White-crowned Sparrows Zonotrichia leucophrys oriantha (Baptista & King 1980, Chilton 2003).

More broadly, our findings suggest that different parts of the songs of Daurian Redstarts have evolved along independent trajectories, one resulting in a subtle dialect or mosaic pattern, and the other in a distinctly clinal pattern. As far as we know, only one other study has documented different patterns of geographic variation from separate parts within songs: in a study of Hermit Thrushes Catharus guttatus across a continental scale, Roach & Phillmore (2017) showed that quantitative variation in note frequency and timing diverged in different ways for opening and later song parts. These authors, however, did not sample enough subpopulations to assess whether variation in different song components would be considered clinal or as dialects. Another distinguishing feature of our study is that it focused on the presence or absence of specific note types, which may wax and wane in their relative frequencies as they are favoured or disfavoured by cultural evolution (e.g. Lynch 1996, Payne 1996). Our findings also complement a study on Chestnut-sided Warblers Dendroica pensylvanica (Byers et al. 2010), which showed that two distinct types of accented- and unaccented-ending song evolved at markedly different rates; unaccented-ending songs were rapidly replaced, whereas song types of accented-ending songs were changed little.

To conclude, it is unknown how different song components of the Daurian Redstart have evolved in such different ways. On a population level, steady cultural drift and consistent low-level migration of birds between populations would be a likely factor for gradual, spatially structured variation of songs and syllable diversity between neighbouring populations. The clinal pattern of song syllables supports this model of evolution. At the same time, however, the mosaic pattern of whistles in these same songs suggests more of a process of geographic isolation, and less exchange among populations. How do we reconcile these possibilities? One place to start would be to presume that learning and resulting cultural transmission of whistles is more accurate than it is for syllables (Harbison et al. 1999). However, we also should not exclude the possibility of distinct selective pressures acting on the two song components, which would require us to consider additional factors such as genetic variation (Lipshutz et al. 2017, Wilkins et al. 2018), morphology (Derryberry et al. 2018), sexual selection (Read & Weary 1990, Lipshutz et al. 2017, Wilkins et al. 2018, Chiver & Schlinger 2019), and habitat differences (Tobias et al. 2010, Greig et al. 2013) for which we have no primary data. Experimental studies of song function could also provide useful insights. In any case, a better understanding of factors influencing the causes and maintenance of multivariate geographic song variation will require more studies both descriptive and experimental in nature.

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