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Avian Behavior, Ecology, and Evolution

Regional song dialects of the Ruby-crowned Kinglet

Dialectos regionales del canto del Reyezuelo Rubí

Edward R. Pandolfino and *Lily A. Douglas* [1]

ABSTRACT. We used archived recordings of Ruby-crowned Kinglet (*Corthylio calendula*) songs to examine characteristics of the song, repertoire size, and regional dialects across the species' breeding range and to assess possible cultural evolution in dialects. Using recordings of 313 individuals, we confirmed that individuals have a single song type and that there are distinct regional song dialects. Our examination of phrases that form the last of this species' 3-part song revealed 43 different phrase types. We defined seven regions based on geographic features, ecoregions, and obvious clustering of particular phrase types. An eighth region corresponded to the published range of the subspecies *C. c. grinnellii*, coastal southern Alaska and the British Columbia coast. In each of those regions, two to three phrase types dominated and were found exclusively or primarily within a single region. Our finding of regional dialects confirms that the song of the Ruby-crowned Kinglet is, at least with respect to this phrase, learned rather than innate. In species, such as this kinglet that sing during migration or in their non-breeding range, mapped dialects can help reveal migration strategy and migratory connectivity. Monitoring changes in dialects over time can confirm cultural evolution and shed light on both the timing and location of song learning.

RESUMEN. Utilizamos grabaciones en repositorios de cantos del Reyezuelo Rubí (*Corthylio calendula*) para examinar las características del canto, el tamaño del repertorio y los dialectos regionales a lo largo del área de reproducción de la especie y para evaluar la posible evolución cultural de los dialectos. Utilizando grabaciones de 313 individuos, confirmamos que los individuos tienen un único tipo de canto y que existen distintos dialectos regionales de canto. Nuestro examinación de las frases que forman la última parte del canto de esta especie que está dividido en tres partes reveló 43 tipos de frases diferentes. Definimos siete regiones basadas en características geográficas, ecorregiones y agrupaciones evidentes de tipos de frases particulares. Una octava región correspondía al área de distribución publicada de la subespecie *C. c. grinnellii*, el sur de Alaska y la costa de la British Columbia. En cada una de estas regiones, dominaban de dos a tres tipos de frases y se encontraban exclusiva o principalmente en una sola región. Nuestro hallazgo de los dialectos regionales confirma que el canto del C. calendula es, al menos con respecto a esta frase, aprendido más que innato. En especies, como este reyezuelo, que cantan durante la migración o en su área de distribución no reproductiva, los dialectos mapeados pueden ayudar a revelar la estrategia de migración y la conectividad migratoria. El seguimiento de los cambios en los dialectos a lo largo del tiempo puede confirmar la evolución cultural y arrojar luz sobre el momento y la ubicación del aprendizaje del canto.

Key Words: *cultural evolution; phrase types; repertoire; Ruby-crowned Kinglet; song; song dialects; song learning*

INTRODUCTION

Confirmation that a species has distinct regional song dialects has important implications for understanding that species' natural history. Such dialects can help reveal when and where song is learned, the relative degree of philopatry or natal dispersal, and patterns of migration to and from the non-breeding range. Fundamentally, the presence of dialects demonstrates that a species' song, or at least the portion of the song that shows regional variation, is probably learned rather than innate (Krebs and Kroodsma 1980, Kroodsma 2004, Catchpole and Slater 2008). Variations in these dialects geographically can help reveal the extent of interaction between populations or subspecies and possibly reveal early stages of speciation (Marler and Tamura 1962, Nottebohm 1969, Baker 1975, Slabbekoorn and Smith 2002, Dingle et al. 2010, Pandolfino and Pieplow 2015) where differences in song dialect could create a barrier to interbreeding (Mortega et al. 2014).

In species that sing during migration and/or on the wintering grounds, song dialects can provide a non-invasive way to investigate migratory pathways, strategies, or connectivity. This approach has been used to study migration of the Puget Sound subspecies of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*; DeWolf and Baptista 1995) and the Golden-crowned Sparrow (*Z. atricapilla*; Pandolfino and Douglas 2021). Song dialect variation among Common Yellowthroat (*Geothlypis trichas*) populations was used to reveal effects of geographic isolation and morphology on song (Bolus 2014). Mapping of dialects also allows one to test the observations of Podos and Warren (2007) that long distance migrants should have large dialect regions as confirmed by Shizuka et al. (2016) for the Golden-crowned Sparrow. Having well-mapped song dialects over time can also reveal cultural evolution in song (Planqué et al. 2014), as recently demonstrated by Otter et al. (2020) for the White-throated Sparrow (*Z. albicolis*). Knowing the distribution of dialects on the breeding and wintering grounds can confirm song learning away from the natal area.

Saunders (1919) observed that the songs he heard from Ruby-crowned Kinglets (*Corthylio calendula*) wintering in the eastern U.S. sounded different from the songs in their Montana breeding range, chiefly in the third part of their three-part songs. However, this has never been confirmed, and there are no studies of song dialects in this species. There are two recognized subspecies of this kinglet, nominate *C. c. calendula* and *C. c. grinnelli*, considered resident from coastal southern Alaska and south

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along the British Columbia coast (Swanson et al. 2021), and the songs of these taxa have not been compared. Further, the song repertoire of the Ruby-crowned Kinglet has not been investigated, though Pieplow (2017) speculated that individuals may use only a single song type. Fahmy and Wilson (2020) observed no change in song type in response to simulated intruders (using playback of different kinglet songs), consistent with a single song repertoire.

Assessing the presence of dialects or other aspects of song across the entire range of a widely distributed species is practically impossible without the use of community science resources. The recent work of Searfoss et al. (2020) characterizing song behavior of the Chipping Sparrow (*Spizella passerina*) throughout its range, Diblíková et al. (2018) mapping song dialects of the Yellowhammer (*Emberiza citrinella*) in Europe, Bolus (2014) on Common Yellowthroat dialects, and of Otter et al. (2020) on evolution in White-throated Sparrow dialects provide recent examples. Similarly, we chose to take advantage of the large archives of song recordings available from xeno-canto (https://www.xeno-canto.org) and the Macaulay Library (https://www.macaulaylibrary.org/) to determine if Ruby-crowned Kinglets show distinct regional dialects across their breeding range and to assess the song repertoires of individual birds. We also used the available recordings to investigate possible cultural evolution in dialects of the easternmost breeders.

METHODS

Recordings used

We obtained all recordings available from xeno-canto and the Macaulay Library of Ruby-crowned Kinglet songs from throughout the species' breeding range recorded between 15 May and 31 July. These included recordings made between 1950 and 2021. For our analyses, we omitted any recordings obtained after playback of song or of such poor quality that assessment was impossible. When multiple recordings from the same location, date, and recordist were available, we assumed they were of the same individual unless noted otherwise. In such cases, we used just one of those recordings.

Terminology

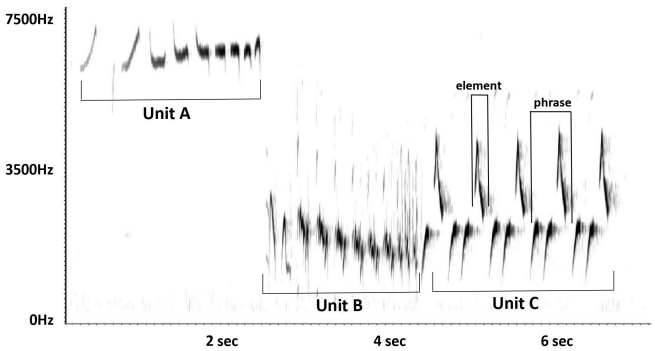
Because terms used for portions of bird song, such as phrase, syllable, element, etc., are used inconsistently and often interchangeably by different authors, it is important to clearly define terminology. In our case, we chose the term "element" for a sound that produced a single continuous trace on a spectrogram (Catchpole and Slater 2008), "phrase" for a repeated set of elements, and "unit" for each of the three distinct parts of the Ruby-crowned Kinglet song (Fig. 1). We chose the term unit for consistency with the work of Päckert et al. (2003) that compared songs of different kinglet species and labeled these as Units A, B, and C for the Ruby-crowned Kinglet to avoid confusion with those authors' use of numbers to label units. Other terms used are defined below:

Phrase type: A phrase composed of a set of elements that was qualitatively distinct by visual inspection from other phrases in the recordings we used.

Doublet, triplet, etc.: Refers to the number of elements in a phrase. We found that phrase types could consist of two, three, or four elements and that the number of repeats of an element in a given phrase type could differ among individuals or even among successive songs from one individual.

For our purposes we defined dialects as macrogeographic, rather than microgeographic (Mundinger 1982, Marler 2004) variation in song. Microgeographic variation produces hard boundaries between specific song types confined to small areas. Macrogeographic variation involves larger areas in which some song elements are shared by many, though not all, individuals within that area. Thus, the use of a given phrase type in Unit C constitutes a song dialect for that individual.

Fig. 1. Spectrograph of a typical Ruby-crowned Kinglet (*Corthylio calendula*) song illustrating the terminology applied to different parts of the song.

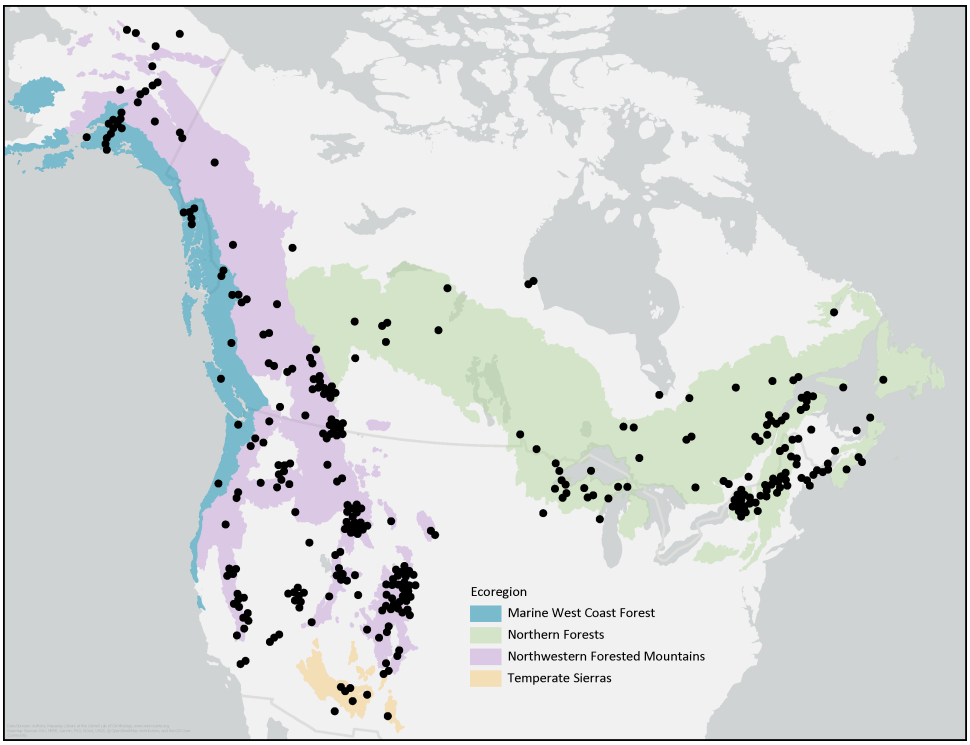


Analyses and assignment of phase types and geographic regions

We reviewed recordings of songs from 313 individuals, which included 1758 examples of full song. The mean number of full songs per recording was six (range 1-105) and seven recordings included only song fragment(s) including Unit C. Most of the breeding range of this kinglet was well-represented by these recordings, with the exception of the boreal habitats of the southern Northwest Territories and the northernmost portions of Alberta, Saskatchewan, Manitoba, Ontario, and Quebec (Fig. 2) where relatively few recordings were available. Appendix 1 (available at https://doi.org/10.6084/m9.figshare.19952822.v1) includes metadata for each recording used.

We used Raven Pro software (KLYCCB 2022) to examine each song or song fragment in these recordings, comparing successive songs to each other for each individual. To assess regional variation, we chose to focus on the phrases that compose the final unit (Unit C) because these phrases are consistently the loudest and most distinct portions of the song. This unit is also missing from the much shorter song of female Ruby-crowned Kinglets (Pieplow 2017, Swanson et al. 2021). None of the recordings used mentioned that any examples of female song were included, and we assumed that all songs were from males. Also, Saunders' (1919) observation of differences between kinglet song from the eastern U.S. compared to that heard in the west, cited that unit as the source of difference. Further, that unit was given independently of full song in 85% of all recordings that included more than one full song, suggesting that this unit may be important for communication.

Fig. 2. Locations of all Ruby-crowned Kinglet (*Corthylio calendula*) recordings used.



To identify the various phrase types, we visually examined the phrases that compose Unit C for each recording and assigned a phrase type number to each unique type. We identified 43 different phrase types. Figure 3 includes examples of the 10 most frequently encountered phrase types in our data set. Examples of the other phrase types, many present in only one or two recordings, are in Appendix 2 (available at https://doi.org/10.6084/m9.figshare.19952888.v1). Appendix 3 (available at https://doi.org/10.6084/m9.figshare.19952936.v1) includes three representative examples of each of the most common phrase types to show variation among recordings. We identified the phrase type for each individual in a blind review to eliminate any possibility of unintentional bias and one of us (ERP) assigned all phrase types. That is, all recordings were coded before review such that the location of each recording was unknown during the assignment to a phrase type. Our qualitative method of assigning phrase types resulted in some similar phrase types being classified as unique types. For example, phrase types 19 and 29 (Fig. 1), phrase types 28 and 38 (Appendix 2), and phrase types 21 and 40 (Fig. 1 and Appendix 2, respectively) differed only in the frequency range and specific shape of the elements. It is possible that these similar phrase types are variations on a single type.

We identified seven regions for comparison based on a combination of ecoregion type (Commission for Environmental Cooperation 1997), geographic features, and the observed distribution of phrase types, attempting to encompass areas in which certain phrase types were most prevalent. An eighth region was defined based on the published range of the subspecies *C. c. grinnelli* (Swanson et al. 2021), which also corresponded well to one ecoregion (Marine West Coast Forest). The regions used are described below and shown in Figures 4 and 5:

- East (mainly boreal forest habitats from western Quebec east);
- North Central (boreal forests from northern Alberta east to western Quebec and south into northernmost Minnesota, Wisconsin and Michigan);
- Interior Alaska (north of the southern coast);
- North Rockies (northwestern forested mountains from Yukon Territory into southern British Columbia and Alberta);
- Central Rockies (forested mountains from southern British Columbia/Alberta to Wyoming, and east to South Dakota);
- South Rockies (from Colorado south into Arizona and New Mexico);
- West (from the western edge of the Rockies west to the Pacific Coast, including the Wasatch and Unita ranges of Utah).

RESULTS

Song structure

Our qualitative review of the songs from 313 individuals showed no examples of deviation from the basic Ruby-crowned Kinglet

Fig. 3. Examples of the 10 most frequently recorded phrase types.

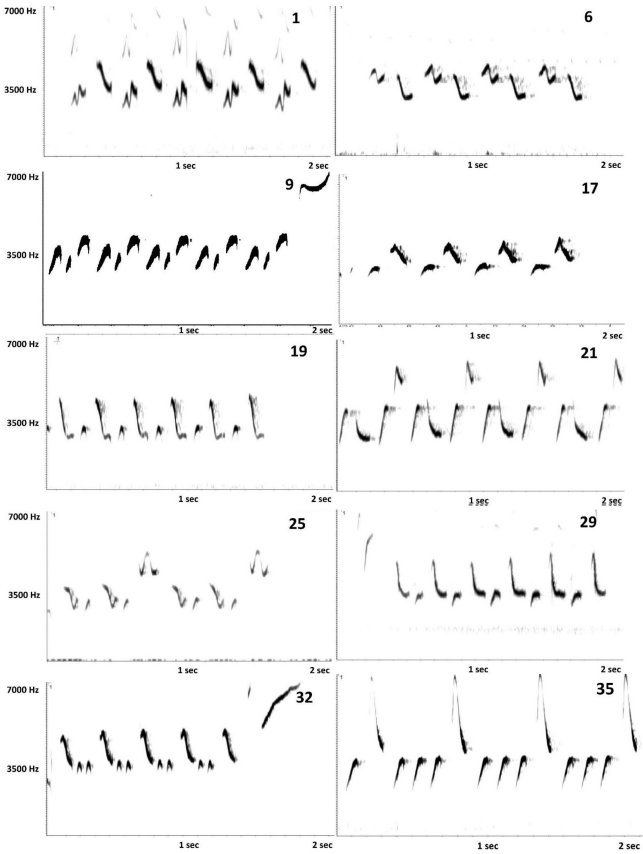
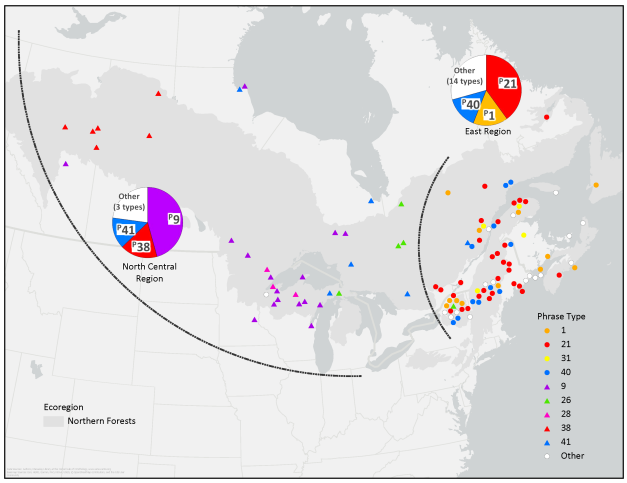


Fig. 4. Recording locations and phrase types of songs recorded in the eastern and north-central parts of the Ruby-crowned Kinglet's (*Corthylio calendula*) range. Dotted lines delineate regions based on clustering of phrase types, ecoregion, and geographic features. Pie charts for each region show the relative abundance of the most common phrase types in that region. The numbers in the charts (preceded by a superscript "p") refer to the phrase type.



song structure described by Saunders (1919), Borror (1970), and Pieplow (2017). Each song began with a series of high-pitched elements that accelerated though Unit A, followed by Unit B composed of a set of two to four different phrases, with each phrase usually delivered in a series, ending in Unit C composed a series of repeated phrases (Fig. 1). Occasionally the song was preceded by a few introductory notes, and sometimes followed by a final, often buzzy element.

Regional dialects

We found distinct regional dialects based on comparisons of the phrases that comprise Unit C of the song across the breeding range (Figs. 4 and 5). Each of the eight regions we defined was dominated by two or three phrase types. These dominant types accounted for more than 70% of types found in any region, ranging from the East where three phrase types comprised 71% of all songs, to the range of *C. c. grinnelli* where two types accounted for 95% of the songs.

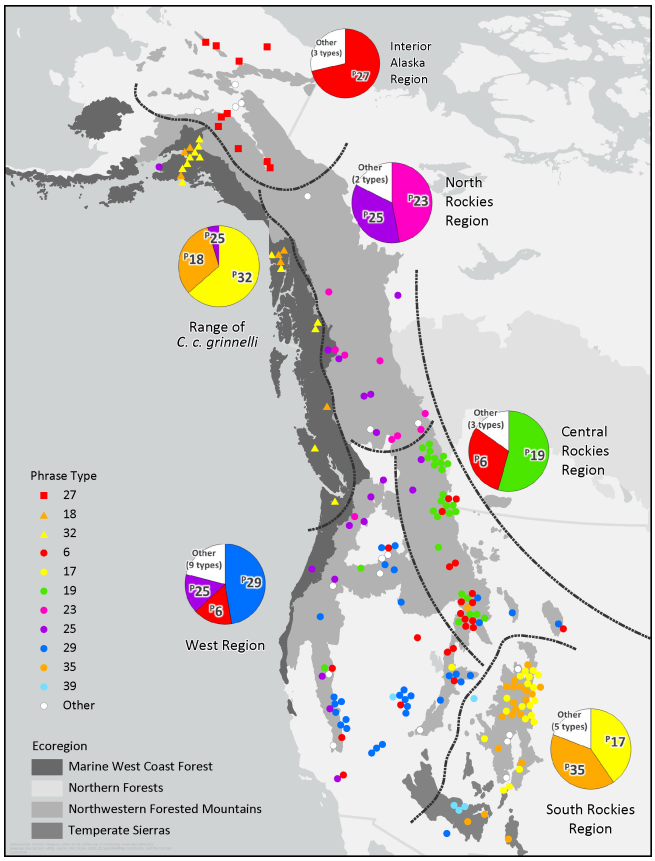
In the East, phrase types 21, 1, and 40 were dominant. Of the 14 other types observed there, 10 were represented by single examples. In the North Central region, phrase type 9 represented nearly half of all types with 2 others, 38 and 41, comprising another 30%. Ten of the 14 phrase types recorded in Interior Alaska were type 27. Phrase types 23 and 25 comprised 82% of all types in the North Rockies. Likewise, the Central Rockies were dominated by 2 phrase types, 19 and 6, which accounted for 85% of all types. Phrase types 17 and 35 represented 81% of the types recorded in the Southern Rockies. The West region included examples of 12 different phrase types but a single type, 29, was found in 47% of the recordings with types 25 and 6 accounting for another 32%. Within the range of the subspecies *C. c. grinnelli*, 21 of the 22 individuals recorded used 1 of 2 phrase types (32 or 18) and those 2 types were not observed anywhere outside that range.

Of the 43 phrase types, 32 (74%) were restricted to a single region, and 9 other types were found only in 2 or 3 adjacent regions. Exceptions included the widespread phrase type 25, which was found in 4 of the 6 western regions from Alaska to southern California and type 19, a predominantly western phrase type that occurred as a single odd example in the east near Whitneyville, Maine on the 31 May 1998. This most likely represents a vagrant record because long distance vagrants of the Ruby-crowned Kinglet have been documented as far the Azores, Iceland, Ireland, and Scotland (BOURC 2022).

Song repertoire

We did not find a single recording suggesting that individual Ruby-crowned Kinglets possess more than one song type. Our review included 39 recordings with more than 10 examples of full song from a single individual, 13 recordings with more than 20 songs, and 3 with more than 30 songs. The only variation noted among the songs of individual kinglets was in the number of repetitions of a phrase. However, the basic structure and the specific phrases and elements used did not vary through any of the singing bouts recorded. Two sets of recordings from Alaska using stationary autonomous recording units covered periods of

Fig. 5. Recording locations and phrase types of songs recorded in the western part of the Ruby-crowned Kinglet's (*Corthylio calendula*) range. Dotted lines delineate regions based on clustering of phrase types, ecoregion, and geographic features. Pie charts for each region show the relative abundance of the most common phrase types in that region. The numbers in the charts (preceded by a superscript "p") refer to the phrase type.



four (xc535205-210) and eight (xc535202-204) days, presumably recording the same individual, and each set showed no indication of a second song type.

Evidence of possible cultural evolution

Because the use of xeno-canto has increased in recent years, and largely due to the dramatic increase in use of eBird (with all recordings archived in the Macaulay Library), the preponderance of samples we obtained were recorded between 2010 and 2021 (81%, 253 of 313). The East was the only region with adequate numbers of older recordings to allow comparison. We found phrase type 21, the dominant type in that region, in none of the 21 recordings made prior to 2009, but it comprised 56% (30 of 54) of more recent recordings. Conversely, phrase type 1, the most commonly recorded type in that region between 1950 and 2009 (one-third of all examples), was given by only 9% (5 of 54) of the individuals recorded since 2009. Because the recordings we used for this comparison were not made in the same locations in both time periods, it is possible that phrase type 21 was present prior to 2009, but not in locations sampled during that earlier period.

DISCUSSION

A comparison of phylogenies of six members of the genus *Regulus* (when the Ruby-crowned Kinglet was considered a member of that genus) based on genetic data vs. song structure (Päckert et al. 2003) led those workers to speculate that the basic organization and syntax of the songs of this genus are inherent rather than learned. They suggested that the specific elements and phrases composed from those elements were probably learned. Our data confirming that certain phrase types are shared by many individuals in a given region, and not found in other regions, establishes the presence of regional dialects in the Ruby-crowned Kinglet. The presence of such regional dialects suggests that the phrases of the final unit (Unit C) are learned. Analysis of other phrases may show that they are learned as well.

We were not able to explicitly confirm the observation of Saunders (1919) that eastern birds primarily give songs with Unit C phrases consisting of triplets, whereas in the west (based only on observations in Montana) these phrases were doublets. The two phrase types most common in Montana were 19 and 6 and, indeed, both are doublet phrases. The major phrase types in the East are 1, 21, and 40. Phrase type 1 is a doublet, while 21 and 40 are both composed of four elements. Because Saunders (1919) did not have the benefit of spectrograms and characterized these phrases from memory and transcribed them into musical notation, he may have been unable to detect the four-element nature of those last two phrase types. It is also possible that song dialects and the dominant phrases have changed over time. Indeed, we found evidence for changes in some phrase types over time in the East. Whether those changes were the result of cultural evolution (which applies only to acquired differences) or an artifact of incomplete sampling, is not possible to say.

Two of our findings, the widely variable distribution of some phrase types and the evidence of cultural evolution among eastern breeders, may help reveal some unusual aspects of song learning among Ruby-crowned Kinglets. We found some phrase types widely distributed such as types 25 and 6 with examples found as much as 3750 km and 1670 km apart, respectively. This is consistent with the findings of Podos and Warren (2007) that long-distance migrants tend to have widespread dialect ranges because of the potential for wider natal dispersal due to stopping short of, or over-flying natal breeding areas. Other phase types we noted, such as 17 and 40, occurred within relatively small areas with the largest separations less than 900 km. Because most small passerines rarely breed more than a few km from their natal areas (Sutherland et al. 2000, Newton 2003), natal dispersal seems less likely to be the mechanism behind the widest ranges of some phrase types. Fayet et al. (2014) found that cultural diversity in the songs of the Great Tit (*Parus major*) within a small area was largely driven by dispersal or immigration. However, an alternative mechanism for very large dialect ranges could be song-learning in the wintering range. If Ruby-crowned Kinglets can learn song on the wintering grounds, where birds from widely separated breeding regions may intermix, this would provide a basis for dialect types to disperse over large areas. This could also help explain why the range of *C. c. grinnelli* had the least diversity of song types of any of the regions we defined. That subspecies is considered non-migratory, meaning that birds of that taxon may not be exposed to the variety of song in winter that the highly migratory nominate subspecies (which breeds in all other regions) encounters.

In nearly all studies of song learning in birds, the sensitive periods for young birds to learn their song were during the nestling/fledgling stage and the following spring when they have moved into breeding areas (Catchpole and Slater 2008). There is, however, evidence that some species can continue to learn and modify their songs into late fall or winter, when birds have moved into their wintering range. Both the resident Nuttall's White-crowned Sparrow (*Z. l. nuttalli*; DeWolfe et al. 1989) and the migratory Mountain White-crowned Sparrow (*Z. l. oriantha*; Baptista and Morton 1988) were able to learn new song elements well beyond the nestling/fledgling stages. Nordby et al. (2001) found that young Song Sparrows (*Melospiza melodia*) learned from live tutors well into late fall of their natal year. An Old World, transequatorial migrant, the Marsh Warbler (*Acrocephalus palustris*), incorporated song elements from African species heard in winter into their adult songs recorded in the breeding range (Dowsett-Lemaire 2008). DeWolfe and Baptista (1995) found that the resident Nuttall's White-crowned Sparrows learned elements of the migratory Puget Sound subspecies song when the two taxa intermixed in winter. However, those elements did not persist in the adult populations. The rapid and dramatic example of cultural song evolution described by Otter et al. (2020) in the White-throated Sparrow appeared to have been the result of learning on the wintering grounds where different breeding populations intermixed. And Chipping Sparrows were able to learn their crystallized song very quickly in their first spring on the breeding grounds (Liu and Nottebohm 2007).

Our observation that Unit C was often given independently of the other song parts may suggest that it has some additional importance in communication beyond the full song, perhaps placing added selective pressure on this unit compared to others. This may warrant further study of the role of this unit in the Ruby-crowned Kinglet's natural history. For example, it would be of interest to determine if certain types were associated with reproductive success, female responsiveness, or enhanced territory defense.

Thus, both the variable distribution of some phrase types and the possible cultural song evolution we observed could be the result of song learning in the non-breeding range of the Ruby-crowned Kinglet. Because this species sings in migration and, to a lesser extent, on the wintering grounds (Pieplow 2017; E. R. Pandolfino, personal observation), this hypothesis could be tested by mapping the migration and wintering locations of this species using phrase types and determining whether these observations might be explained by learning from discrete breeding populations. Such studies could also reveal migration strategies and migratory connectivity in this kinglet.

If such studies reveal that the Ruby-crowned Kinglet uses a leapfrog migration strategy, in which northern breeders have much longer migrations than southern ones (Welty 1982, Newton 2008), a different mechanism for wide dispersal of dialects may be a factor. Podos and Warren's (2007) observation that long-distance migrant species had larger dialect regions than short-distance migrants might also apply to different populations within a single species. In this case, the most widely dispersed dialect may belong to the most northerly breeders. However, as Podos and Warren (2007) also noted, timing of song learning, as discussed above, could also affect dialect dispersal.

Our finding of regional song dialects for the Ruby-crowned Kinglet supports the assumption that at least a portion of the song is learned rather than innate. These mapped dialects may prove useful for understanding when and where this species learns its song. Dialect maps of this type, in species that sing during migration or in their non-breeding range, provide a non-invasive approach to study migratory strategy and connections.

Responses to this article can be read online at:
https://journal.afonet.org/issues/responses.php/120

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Data Availability:

No data/code used.

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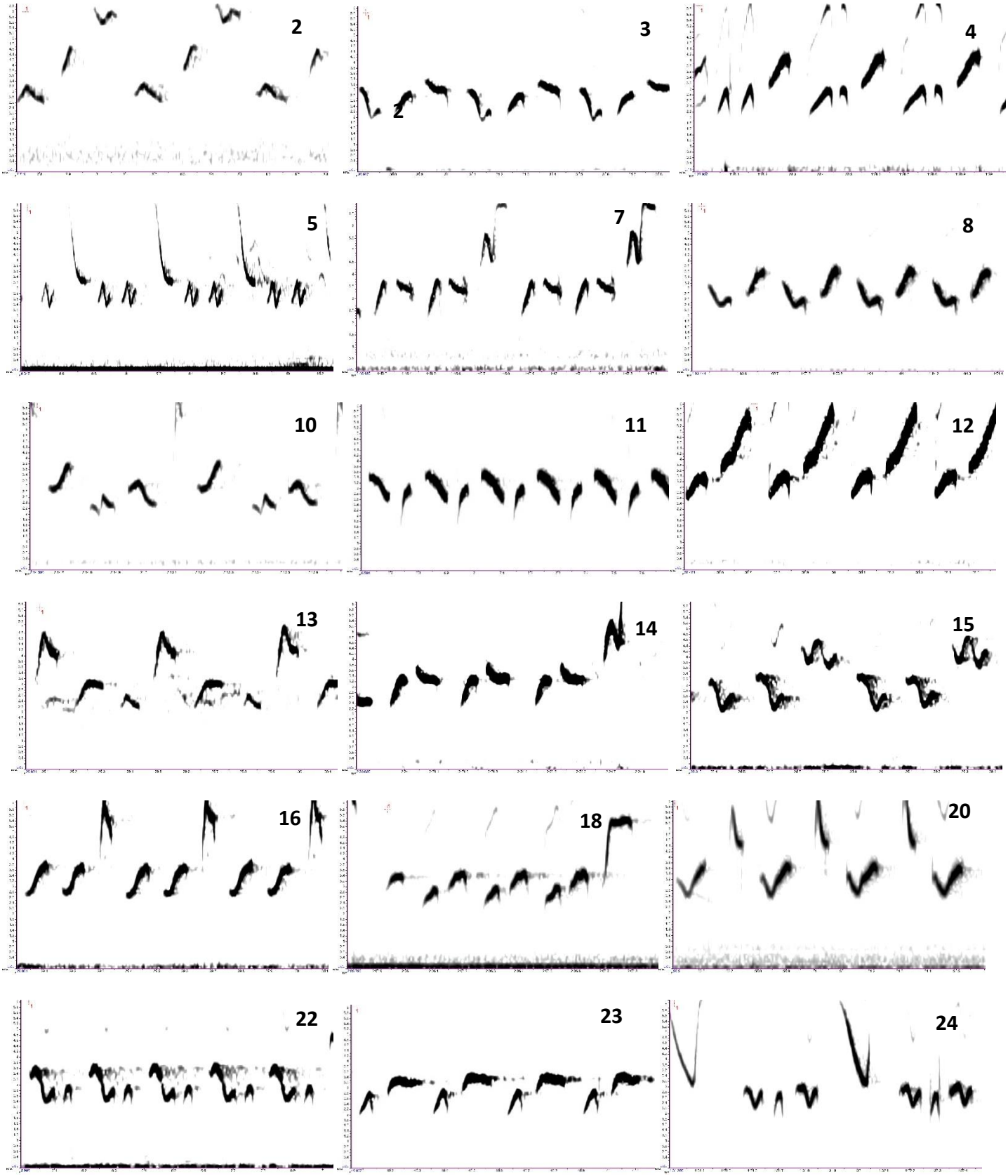
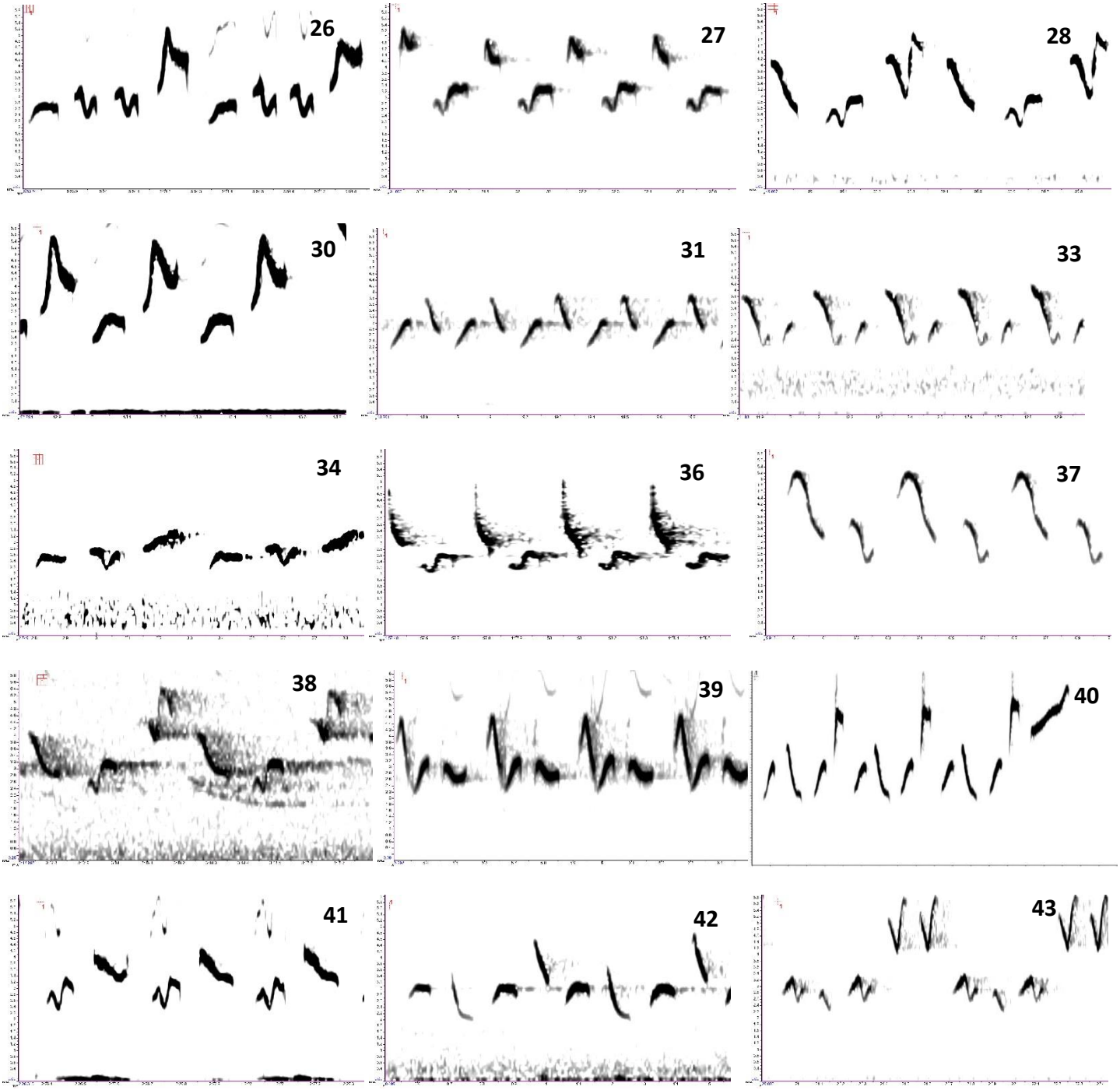
Appendix 1. Appendix A. Metadata for all recordings used. Catalog numbers preceded by "xc" are recordings from xeno-canto, all others from Macaulay Library.

Please click here to download file 'appendix1.xlsx'.

Appendix 2. Examples of the 33 less common phrase types. All scales are approximately equal (0-7000 Hz, and 0-2 seconds).

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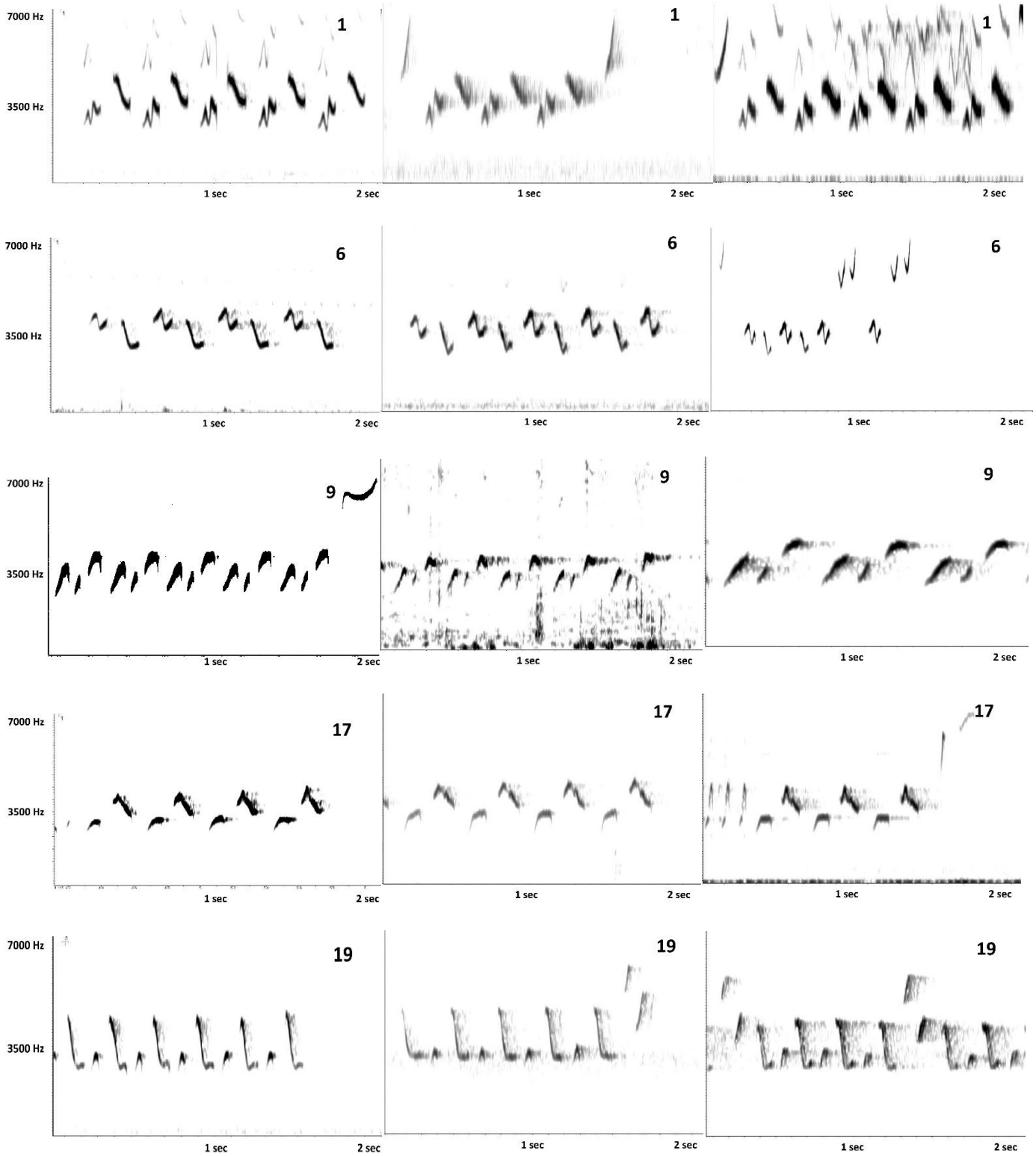
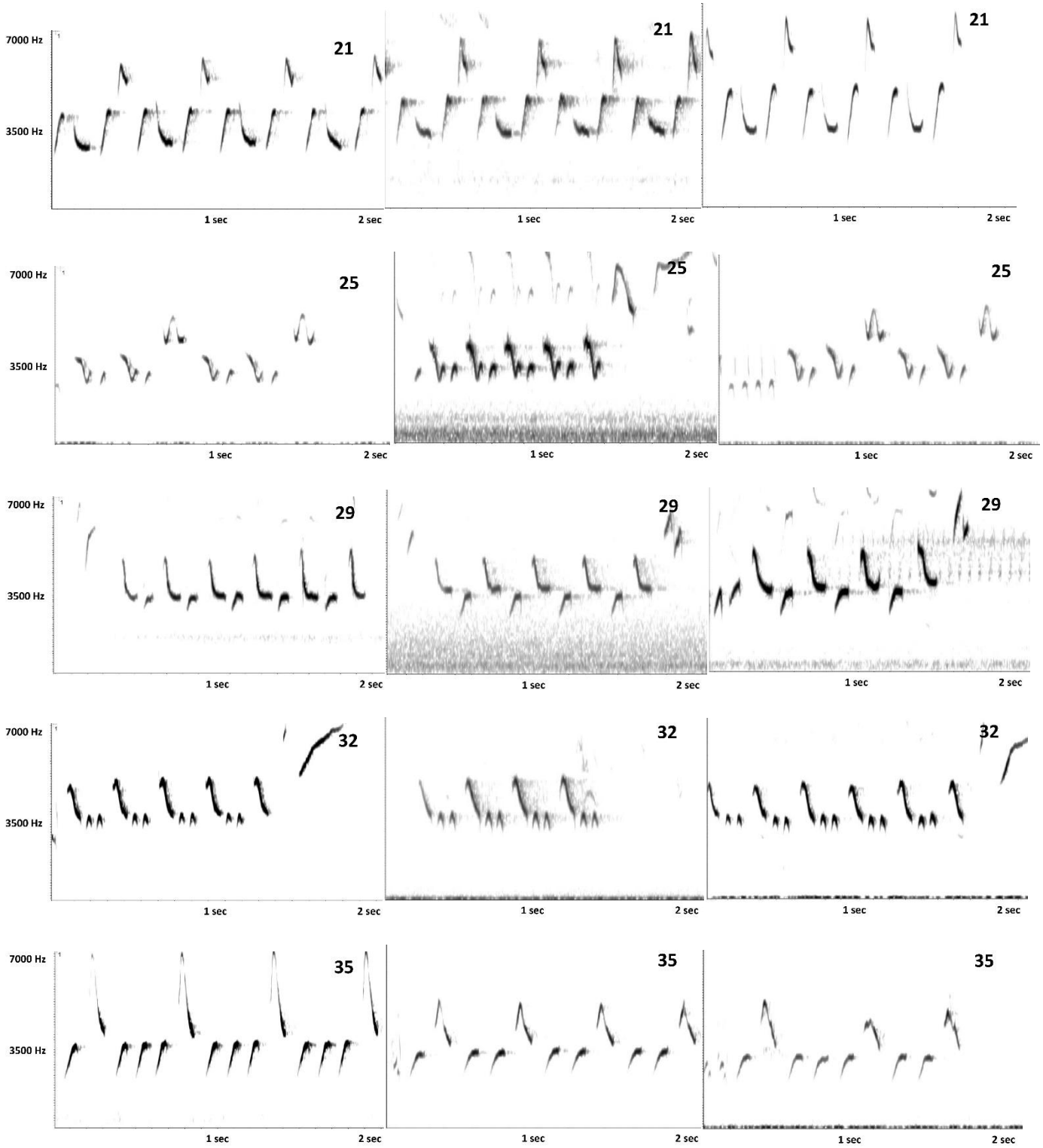
Appendix 3. Examples from different individuals of the ten most common phrase types.

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