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RESEARCH ARTICLE

Range-wide patterns of geographic variation in songs of Golden-crowned Sparrows (*Zonotrichia atricapilla*)

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ABSTRACT

Discrete geographic variation, or dialects, in songs of songbirds arise as a consequence of complex interactions between ecology and song learning. Four of the five species of *Zonotrichia* sparrows, including the model species White-crowned Sparrow (*Z. leucophrys*), have been studied with respect to the causes and consequences of geographic variation in song. Within White-crowned Sparrows, subspecies that migrate farther have larger range size of dialects. Here, we assessed geographic patterns of song variation in the fifth species of this genus, the Golden-crowned Sparrow (*Z. atricapilla*). We analyzed field-recorded songs from 2 sampling periods (1996–1998 and 2006–2013) covering most of its breeding range in western North America. All songs began with a descending whistle and most songs consisted of 3–4 phrases that contained combinations of whistles, buzzes, and trills. We identified 13 discrete song types based on unique sequences of phrase types and frequency changes between phrases. Over 90% of individuals sang 1 of 5 song types, and we found clear dialect structure composed of these 5 common song types. The geographic range of dialects spanned large distances (500 to 1,700 km), resembling the geographic structure of dialects in the long-distance migrant Gambel's White-crowned Sparrow (*Z. l. gambelli*), though locations of dialect boundaries differ between species. Because both Golden-crowned Sparrows and Gambel's White-crowned Sparrows migrate similarly long distances, our study provides support to the hypothesis that dialect range size correlates with migration distance. We found little evidence of change in dialect composition in 4 populations that were sampled 15 years apart, which suggests that the dialect structure is stable across multiple generations. Our study opens the door for further comparisons to investigate links between ecology and the emergence of song dialects in this well-studied genus.

Keywords: White-crowned Sparrow, song dialects, cultural evolution

Patrones de variación geográfica a lo largo de todo el rango en los cantos de *Zonotrichia atricapilla*

RESUMEN

La variación geográfica discreta, o los dialectos, en los cantos de las aves canoras se originan como consecuencia de interacciones complejas entre la ecología y el aprendizaje de los cantos. Cuatro de las 5 especies de *Zonotrichia*, incluyendo la especie modelo *Z. leucophrys*, han sido estudiadas con respecto a las causas y consecuencias de la variación geográfica en el canto. Al interior de la especie *Z. leucophrys*, las subspecies que migran más lejos tienen dialectos con rangos más amplios. En este trabajo evaluamos los patrones de variación del canto en la quinta especie de este género, *Z. atricapilla*. Analizamos cantos grabados en el campo de dos períodos de muestreo (1996–1998 y 2006–2013), cubriendo la mayor parte de su rango reproductivo en el oeste de América del Norte. Todos los cantos comienzan con un silbido descendente y la mayoría de los cantos consistieron en 3–4 frases con combinaciones de silbidos, zumbidos y trinos. Identificamos 13 tipos discretos de cantos basados en secuencias únicas de tipos de frases y en cambios de frecuencia entre frases. Más del 90% de los individuos cantaron uno de los 5 tipos de cantos, y encontramos una clara estructura del dialecto compuesta por estos 5 tipos de cantos comunes. El rango geográfico de los dialectos abarcó grandes distancias (500 a 1,700 km), asemejándose a la estructura geográfica de los dialectos de la especie migratoria de larga distancia *Z. l. gambelli*, aunque las localidades de frontera de los dialectos difirieron entre especies. Debido a que *Z. atricapilla* y *Z. l. gambelli* migran ambas largas distancias, nuestro estudio apoya la hipótesis de que el tamaño del rango del dialecto se correlaciona con la distancia de migración. Encontramos poca evidencia de cambios en la composición del dialecto en cuatro poblaciones que fueron muestreadas con una diferencia de 15 años, lo que sugiere que la estructura del dialecto es estable a través de varias generaciones. Nuestro estudio abre la puerta a comparaciones adicionales para investigar los vínculos entre la ecología y la emergencia de dialectos del canto en este género bien estudiado.

Palabras clave: dialectos del canto, evolución cultural, *Zonotrichia atricapilla*, *Zonotrichia leucophrys*

INTRODUCTION

Patterns of variation in songs of oscine passerine birds, those that learn songs through acoustic experience, provide unique insights at the intersection of evolutionary and cognitive research (Marler 1990). For example, the interaction between song learning processes and patterns of dispersal can determine the geographic patterns of song variation, including the formation of song dialects (Podos and Warren 2007). Moreover, small errors in learning can lead to cultural evolution of song across time within populations, leading to song divergence among populations that are culturally separated (Planqué et al. 2014). Because bird song functions in courtship and territoriality, there has been interest in whether differences in song among populations can promote speciation (Baker and Cunningham 1985, Slater 1989, Slabbekoorn and Smith 2002, Lachlan and Servedio 2004, Olofsson et al. 2011).

Studies of geographic variation in songs of White-crowned Sparrows have been particularly instrumental in understanding the links between ecology, evolution, and cognition. Marler and Tamura (1962, 1964) first demonstrated that the sedentary subspecies of White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) exhibits highly localized song types that vary across populations across the San Francisco Bay area. Their work was followed by many studies on song dialects in this species, defined here as discrete geographic variation in song structure at any spatial scale (summarized in Podos and Warren 2007). Decades of work have now characterized patterns of geographic variation in many songbirds, including 4 of the 5 subspecies of White-crowned Sparrow (e.g., Marler and Tamura 1964, DeWolfe et al. 1974, Baptista 1977, Baptista and King 1980, Baker and Thompson 1985, Nelson 1998, Chilton et al. 2002) and 3 other congeners: the White-throated Sparrow (*Z. albicollis*: Borror and Gunn 1965, Falls 1969, Ramsay and Otter 2015), Rufous-collared Sparrow (*Z. capensis*: Nottebohm 1969, 1975, King 1972, Handford 1988, Loughheed and Handford 1992, Lijtmaer and Tubaro 2007), and Harris' Sparrow (*Z. querula*: Shackleton et al. 1991). Comparisons across subspecies of White-crowned Sparrow have demonstrated a correlation between migration distance and dialect structure: subspecies that migrate farther have larger dialect ranges (Chilton et al. 2002). Meta-analysis by Podos and Warren (2007) provided comparative evidence for a link between migration and the size of dialect regions in a number of species. Thus, comparative studies of subspecies of White-crowned Sparrows have generated important hypotheses about the ecological factors that affect dialect structure.

The patterns of change and stability in geographic variation in oscine bird songs represent an ideal test case of cultural evolution—the process of change in culturally transmitted traits across time leading to population

differentiation (Mundinger 1980, Lynch et al. 1989). Patterns of cultural evolution of song have been investigated in White-crowned Sparrows (Chilton and Lein 1996a, Harbison et al. 1999, Chilton 2003, Nelson et al. 2004) and other species (Lynch et al. 1989, Ficken and Popp 1995, Wright et al. 2008). These studies have demonstrated collectively that (1) cultural transmission of song can lead to long-term persistence of dialects over decades, (2) dialect boundaries can shift over the same time period, and (3) some song phrases are more labile than others.

Here we provide results of the first study of patterns of variation across space and over time in songs of the Golden-crowned Sparrow (*Z. atricapilla*), the only member of *Zonotrichia* for which such variation has not been characterized. The Golden-crowned Sparrow and White-crowned Sparrow are putative sister species, forming a monophyletic group based on allozyme markers (Zink et al. 1991) and multilocus DNA phylogenies (Klicka et al. 2014). However, signatures of mitochondrial haplotype sharing between some populations suggest that hybridization in the recent past could have led to mitochondrial introgression (Weckstein et al. 2001), a pattern that obscures their precise evolutionary relationship. Golden-crowned Sparrows are long distance migrants (Seavy et al. 2012) that share much of their wintering and breeding range with migratory Gambel's White-crowned Sparrows (*Z. l. gambelii*), and thus provide a point of comparison (though not phylogenetically independent) to test hypotheses about the causes of geographical song variation. Specifically, we used large-scale surveys and archived recordings to assess patterns of geographic variation in Golden-crowned Sparrows and test the hypothesis that geographical patterns of variation in their songs correlate with migration distance. This hypothesis predicts that, given their long-distance migration habits, dialect regions in Golden-crowned Sparrows would be relatively large.

For several populations for which we made recordings over a decade apart, we could also test whether dialect composition was stable within sites across generations, as has been shown in White-crowned Sparrows.

METHODS

Study Sites

Golden-crowned Sparrows breed in shrub habitats near treeline in and west of the Canadian Rocky Mountains, and in coastal shrub habitats in Alaska. We collected songs from 32 sites spanning much of the breeding range (maximum distance between sites = 3,100 km) with the exception of portions of Alaska and northern Canada that are not easily accessible by road (Table 1). In some cases, the number of samples per site is limited because some small patches of treeline habitat harbored very few breeding individuals.

TABLE 1. Numbers of Golden-crowned Sparrows whose songs were recorded at localities in Alaska (AK), Yukon (YK), British Columbia (BC), and Alberta (AB). Locality numbers correspond to localities depicted on Figure 2.

Locality	Latitude	Longitude	1996–1998	2006–2013
1. Nome, AK	64.75°N	165.25°W	0	15
2. Homer, AK	59.84°N	151.41°W	0	11
3. Kenai, AK	60.53°N	150.17°W	0	4
4. Seward, AK	60.18°N	149.66°W	0	4
5. North Slope, AK	68.05°N	149.62°W	0	4
6. Hatcher Pass, AK	61.77°N	149.25°W	0	12
7. McCarthy, AK	61.29°N	142.52°W	0	6
8. Kluane, YT	60.97°N	138.42°W	0	1
9. Chilkat Pass, BC	59.74°N	136.63°W	19	15
10. Mt. McIntyre, YT	60.63°N	135.17°W	2	0
11. White Pass, BC	59.66°N	135.12°W	0	12
12. Montana Mt., YT	60.10°N	134.70°W	25	0
13. Juneau, AK	58.18°N	134.22°W	0	4
14. Freer Creek, YT	60.02°N	130.45°W	13	0
15. Stewart, BC	56.17°N	130.05°W	0	11
16. Rancheria Mt., YT	60.15°N	130.00°W	3	0
17. Smithers, BC	54.77°N	127.28°W	10	15
18. Tweedsmuir, BC	52.17°N	125.29°W	0	4
19. Stone Mt., BC	58.62°N	124.67°W	5	11
20. Powder King, BC	55.36°N	122.64°W	0	2
21. Grizzly Den, BC	53.83°N	121.58°W	0	1
22. Manning Prov. Park, BC	49.15°N	120.75°W	1	0
23. McBride, BC	53.34°N	120.12°W	0	12
24. Ambler Ridge, AB	53.93°N	119.25°W	4	0
25. Stearn Mt., AB	53.87°N	119.22°W	9	0
26. Indian Ridge, AB	52.83°N	118.15°W	3	0
27. Marmot Basin, AB	52.75°N	118.12°W	3	0
28. Mt. Edith Cavell, AB	52.65°N	118.03°W	4	5
29. Bald Hills, AB	52.30°N	117.67°W	11	0
30. Opal Hills, AB	52.75°N	117.62°W	2	0
31. Cardinal Divide, AB	52.88°N	117.27°W	1	0
32. Wilcox Pass, AB	52.23°N	117.20°W	0	4

We used several sources of song recordings. Songs were collected by G. C. and assistants at 17 sites in Alberta, British Columbia, and the Yukon, Canada, during 1996–1998. D. S. and assistants collected songs from 18 sites across Alaska, Alberta, British Columbia, and the Yukon in 2007 and 2011. In addition, we included in our dataset songs archived at the Macaulay Library of Natural Sound (recorded in 2006 and 2007 at 4 sites), as well as songs provided by A. P. Rose from McCarthy, Alaska (recorded in 2011 at 1 site) and A. Borker from Nome, Alaska (recorded in 2013 at 1 site). All songs were recorded during the breeding season (May–July). Further details of our sample are provided in Table 1.

Equipment and Recording Protocol

G. C. and assistants recorded songs with Sony TCM-5000EV (Sony Corporation, Tokyo, Japan) cassette tape recorders and Gibson EPM P-650 microphones (Gibson

Brands, Nashville, Tennessee, USA). These recordings were digitized at 44.1 kHz sampling rate with 32-bit precision. D. S. and A. P. Rose used a Marantz PMD-661 (Marantz, Kanagawa, Japan) solid-state digital recorder with a Sennheiser ME67 (Sennheiser, Wedemark, Germany) shotgun microphone with K6 power module (48 kHz sampling rate, 16-bit). A. Borker recorded with a TASCAM DR-05 recorder (TASCAM, Montebello, California, USA) using a Røde VideoMic Pro microphone (44.1 kHz sampling rate, 16-bit; Røde Microphones, Sydney, Australia). All field recordings were saved in .wav format. Accession numbers for recordings provided by the Macaulay Library of Natural Sounds are found in the Appendix. All songs included in the analysis were recorded from territorial individuals during the breeding season. In populations in which individuals were not banded, we avoided recording individuals more than once by sampling at different localities on different days.

Song Analysis

We generated spectrograms of all recordings in Raven Pro (FFT = 1024, Bandwidth = 90 Hz) (available from Cornell Lab of Ornithology at <http://www.birds.cornell.edu/brp/raven/RavenOverview.html>). For each song, we classified the elements for each phrase using the following scheme (see Figure 1): *descending whistle* (whistle with downward frequency modulation); *flat whistle* (whistle with no frequency modulation); *broken whistle* (multiple whistle notes with no change in center frequency); *buzz* (a pulsed, broadband note); and *terminal trill* (a simple note repeated in rapid succession). We also categorized the frequency change between the second and third phrases as ascending, descending, or no change.

For most birds, we measured and classified elements of 3 songs chosen randomly from a single recording of an individual ($n = 240$). In a few cases, we were only able to analyze 1 or 2 songs per individual (2 songs: $n = 18$; 1 song: $n = 11$). We include these individuals in our sample because observations suggest that individuals sing a single predominant song type throughout the season (D. Shizuka personal observation). Previous work on other *Zonotrichia* sparrows suggests that the vast majority of males sing limited repertoires consisting of 1 or 2 song types (Borror and Gunn 1965, King 1972, Lemon and Harris 1974, Baptista 1977, Fotheringham 1995, Chilton and Lein 1996b; but see Shackleton et al. 1991 for slightly larger repertoires in Harris's Sparrows). Moreover, each discrete measure described above was consistent for all individuals for which we had recorded multiple songs: individuals always sang one song type within a recording session (see Results).

Statistical Analysis

We first identified discrete song types using 6 categorical factors at the individual level (phrase type for phrases 1–5

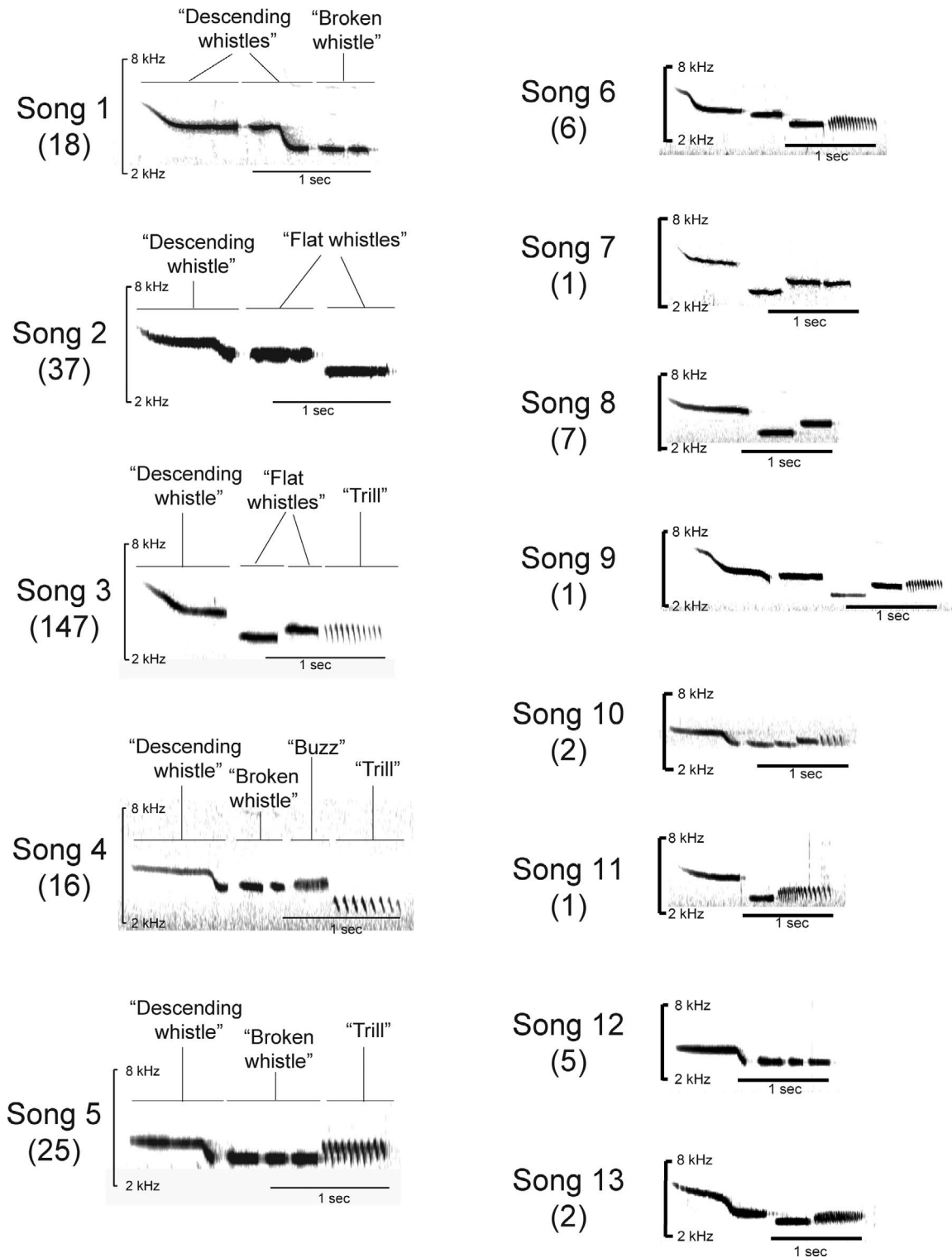


FIGURE 1. Spectrograms of Golden-crowned Sparrow song types. The number in parentheses indicates the number of individuals singing each song type. The 5 songs on the left column are the most common song types, comprising 91% of the sample. The 8 songs on the right column are rarer song types. Phrase types that were used to categorize the songs are indicated for the 5 common songs (also see Table 2).

TABLE 2. Variables used for categorical classification of song types.

Song variant	Number of males	Phrase 1	Phrase 2	Phrase 3	Phrase 4	Phrase 5	Frequency change between whistles in phrases 2 and 3
1	18	DW	DW	BW	N/A	N/A	N/A
2	37	DW	FW	FW	N/A	N/A	Descending
3	148	DW	FW	FW	TR	N/A	Ascending
4	25	DW	BW	BZ	TR	N/A	N/A
5	16	DW	BW	TR	N/A	N/A	N/A
6	6	DW	FW	FW	TR	N/A	Descending
7	1	DW	FW	FW	FW	N/A	Ascending
8	7	DW	FW	FW	N/A	N/A	Ascending
9	1	DW	FW	FW	FW	TR	Descending
10	2	DW	BW	FW	TR	N/A	Ascending
11	1	DW	FW	BZ	TR	N/A	N/A
12	5	DW	BW	N/A	N/A	N/A	N/A
13	2	DW	FW	TR	N/A	N/A	N/A

Abbreviations: DW = descending whistle; FW = flat whistle; BW = broken whistle; BZ = buzz; TR = trill.

and the pattern of frequency change between whistles in phrases 2 and 3; Table 2). This resulted in 13 discrete variants of songs. We checked the robustness of this method with cluster analysis using a mix of 4 categorical and 3 numerical variables (phrase type for phrases 1–4, frequency ratio between phrase 1 and 2, frequency ratio between phrases 2 and 3, and the number of trill notes) and number of clusters determined by *k*-means clustering. This analysis supported the identification of 13 discrete song types, with very high agreement in assignment of individual songs to each cluster (adjusted Rand Index = 0.99; [Supplemental Material, Methods](#); [Supplemental Material, Figures 1 and 2](#)). We report the results of the simpler methods using only categorical variables in the main text.

We assessed the stability of song variation across time by comparing the frequencies of song types at each of 4 sites that were sampled in 1996–1997 and 2011 (Chilkat Pass, Mt. Edith Cavell, Stone Mountain, and Smithers).

RESULTS

Songs of Golden-crowned Sparrows typically consisted of 3 or 4 phrases (with 2 exceptions: Song 9 had 5 syllables and Song 12 had 2 syllables) that always included whistles, and in some populations, trills and/or buzzes. All song types began with an introductory whistle that contained downward frequency modulation (Figure 1).

Using a classification scheme based on phrase types, our global sample of Golden-crowned Sparrow songs ($n = 268$ individuals) was divided into 13 discrete song types (Figure 1). The vast majority of individuals (91.4%) sang 1 of the 5 most common song types, which we designate as Songs 1 through 5 (Figure 1). Within-type variation for these song types are represented in [Supplemental Figure 3](#). Each of

these common song types was performed by the majority of individuals in at least one site (Figure 2). Each of the other 8 rarer songs are designated as Songs 6 through 13 (Figure 1). These were sung by 1–7 individuals (median = 2 individuals). Golden-crowned Sparrows in our sample performed only one song type during the recording session (11.2 ± 2.3 songs per individual, mean \pm SEM; max = 46 songs).

The sizes of dialect regions, defined as the distances between farthest populations with the same dominant dialect, differed among song types (Figure 2). The minimum range of the dialect region for Song 1 was ~ 800 km, assuming continuous distribution of this song type between the 2 populations where this song type was recorded (Nome and North Slope: sites 1 and 5 in Figure 2). The dialect region for Song 2 stretched at least 500 km, from Homer to McCarthy, AK (sites 2 and 7 in Figure 2). Song 3, the largest dialect region detected by our sampling scheme, extended over 1,700 km from Kluane Lake, YT, to Manning Provincial Park, BC (sites 8 and 22 in Figure 2). Songs 4 and 5, which are very similar and could be variants of the same dialect, occurred in spatially discontinuous populations within this range, in the Cassiar Mountains, YT (Montana Mountain, Freer Creek, and Rancheria Mountain: sites 12, 14, and 16 in Figure 2) and in the southern Coast Mountains, BC (Smithers and Tweedsmuir: sites 17 and 18 in Figure 2), respectively. These sites are separated by ~ 620 km, and populations that occurred between these sites were dominated by Song 3.

The predominant song changed very little across the 4 sites that were sampled in both 1996–1997 and 2011 (Table 3). The only new appearance of a common song type was at Smithers, where we recorded 2 individuals singing Song 3 in 2011 but where this song was not detected in 1997. In contrast, the appearance or loss of rare song types occurred at all 4 sites.

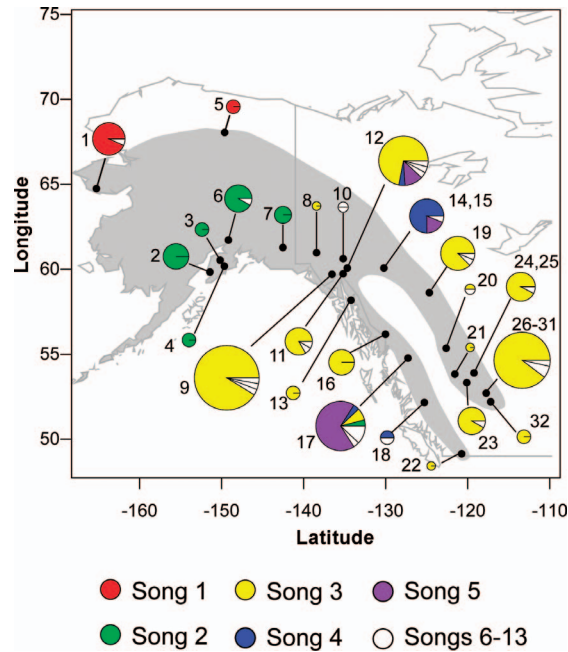


FIGURE 2. The distribution of song types across the breeding range of Golden-crowned Sparrows. The size of the pie chart associated with each sampling site is proportional to the sample size (see Table 1). In each pie chart, the colored wedges indicate the frequency of common song types while the frequency of rare song types are indicated by blank wedges. Site numbers next to pie charts correspond to site numbers in Table 1. For graphical clarity, some sampling sites are aggregated.

DISCUSSION

We provide the first formal description of the songs of Golden-crowned Sparrows, the last of 5 species of *Zonotrichia* sparrows to be characterized in detail. We could divide the songs of Golden-crowned Sparrows into 13 discrete song types that contained unique combinations of phrase types and frequency changes between whistle phrases. Of these 13 song types, the 5 most common song types made up 91% of our sample. The 8 rare song types were rarely shared among individuals in a population (Figure 2). We suggest that the rare song types we recorded are aberrant variants that arise as a result of learning and performance errors.

All Golden-crowned Sparrow song types included an introductory whistle with downward frequency modulation (Figure 1), though we note that there is noticeable

variation in the precise pattern of frequency modulation across individuals (Supplemental Figure 3). In White-crowned Sparrows, the introductory whistle is thought to be an innate component of their song that plays important roles during song development. Individuals that are acoustically isolated during the sensitive period for song learning produce aberrant songs, but these often still contain introductory whistles (Marler 1970). Moreover, White-crowned Sparrows preferentially learn songs that contain introductory whistles (Soha and Marler 2000). The introductory whistle of the Golden-crowned Sparrow could play an important role in species-specific song learning by acting as an innate cue for song recognition. Shizuka (2014) showed that Golden-crowned Sparrow nestlings could discriminate between conspecific songs and White-crowned Sparrow songs at 7–8 days old. It would be interesting to determine whether the frequency

TABLE 3. Comparisons of song types at 4 sites that were sampled 14–15 years apart.

Site	Year	Song 3	Song 4	Song 5	Song 6	Song 8	Song 9	Song 11	Song 12
Chilkat Pass	1996	17	0	0	0	1	1	0	0
	2011	14	0	0	1	0	0	0	0
Smithers	1997	0	1	8	0	0	0	0	0
	2011	2	1	9	0	0	0	1	3
Mt. Edith Cavell	1996	2	0	0	0	2	0	0	0
	2011	5	0	0	0	0	0	0	0
Stone Mt.	1996	5	0	0	0	0	0	0	0
	2011	9	0	0	1	1	0	0	0

modulation in the introductory whistle plays a role in species-level discrimination of song by young Golden-crowned Sparrows.

Prevailing theory suggests that geographic patterns of song variation are influenced by complex interactions between song learning mechanisms and dispersal distance, and that migratory species tend to have larger dialect regions than sedentary species due to their relatively greater mobility during natal dispersal (reviewed in Podos and Warren 2007). Golden-crowned Sparrows are long-distance migrants, with individuals known to travel from the central coast of California to the Alaska Peninsula (Seavy et al. 2012). Thus, we expected that Golden-crowned Sparrows would have relatively large dialect ranges. Indeed, we identified very large dialect structure in Golden-crowned Sparrows with a few distinct song types throughout their breeding range. While the distribution of our sampling sites are spotty in some areas due to inaccessibility (e.g., northern Alaska), we can estimate the extent of dialect regions as the maximum distance between populations that share predominant song types. Based on our sampling scheme, 3 of the 5 common song types covered ranges spanning 500 km (Song 1) and 1,700 km (Song 3). The sizes of these dialect regions are similar to the regional scale of variation in songs of the Gambel's White-crowned Sparrow, a long-distant migratory subspecies with which the Golden-crowned Sparrow shares both wintering and breeding ranges. In Gambel's White-crowned Sparrows, song dialect regions span at least 500 km (Chilton et al. 2002). In contrast, White-crowned Sparrow subspecies with shorter migration distances have correspondingly smaller dialect regions. The Mountain White-crowned Sparrows (*Z. l. oriantha*) exhibit an intermediate migration distance, and their dialect regions can span up to 275 km (Baptista and King 1980, Lein and Corbin 1990, Harbison et al. 1999). The short-distance migrant Puget Sound subspecies of White-crowned Sparrows (*Z. l. pugetensis*) have dialects that span tens of kilometers (Baptista 1977), while populations of the sedentary subspecies (*Z. l. nuttalli*) can contain multiple dialects within 2–3 km (Marler and Tamura 1962, Baptista 1975, Trainer 1983, Baker and Thompson 1985, Cunningham et al. 1987). Thus, the large spatial scale of geographic variation in song in the long-distance migrant Golden-crowned Sparrows generally supports the hypothesis that the sizes of dialect regions correlate with migration distance.

It is worth noting that, while we have focused our analysis on the sequence of phrases in Golden-crowned Sparrow songs to identify discrete song types, there may be other aspects of song structure within song types that also vary geographically. For example, while phrase sequences can vary within as well as across subspecies of White-crowned Sparrows, dialects can also be identified using the

structures of specific syllables (e.g., Marler and Tamura 1962, Baptista 1975, 1977, Baptista and King 1980, Chilton et al. 2002). Further analyses of detailed structures of specific syllables such as the introductory whistle and trills combined with more intensive sampling could reveal more refined understanding of geographic variation in Golden-crowned Sparrow song.

Two of the five common song types (Songs 4 and 5) occurred together in 2 regions over 600 km from each other (Cassiar Mountains and the southern Coast Mountains). Populations between these areas sang Song 3. These song types 4 and 5 are very similar (Figure 1) and may be functional variants of the same dialect. The disjunct distribution of these song types was present in 1996–1997. Unfortunately, the Cassiar Mountain sites (Freer Creek, Rancheria Mountain, and Montana Mountain) were not sampled in 2006–2013, and thus we could not determine whether the distribution of these song types remained stable across the 15-year span of our sampling efforts. There are 2 hypotheses to account for such disjunct distribution of song types: independent cultural evolution and historical changes in song distribution. Independent cultural evolution seems unlikely given that there is scope for much more variation as evidenced by the rare song types detected in our sample. Even so the same 2 song types are predominant songs in 2 different sites. It is more likely that the song dialect regions became disjunct through the invasion and spread of Song 3 in northern Coast Mountains. If so, future song sampling at these sites could reveal the spread of song types as a consequence of cultural evolution.

The most dramatic geographic transition in songs of Golden-crowned Sparrows occurred across 220 km near the Yukon–Alaska border. West of this divide, no birds were observed to incorporate terminal trills (0 of 56 birds recorded), while the vast majority of the birds east of this border performed songs with trills (202 of 212 birds recorded). Whether a mixed-dialect zone between these 2 song forms exists is currently unknown because suitable breeding habitat in this area was not accessible by road. This transition zone is defined by the Wrangell and St. Elias Mountain ranges, which are mostly covered by ice and snow, and is probably sparsely populated by Golden-crowned Sparrows. While this biogeographic gap does not seem to represent a hard boundary in the species' range, it may be enough to limit dispersal across this zone, thus resulting in a large difference in vocal traditions of populations on either side. However, Chilton et al. (2002) showed that Gambel's White-crowned Sparrows sang the same song types across this divide (in Whitehorse, YT, and southeastern Alaska). We cannot say why these ecologically similar species show different patterns of song variation across putative geographic barriers. Perhaps Golden-crowned and White-crowned sparrows use differ-

ent migratory routes, so that certain geographical features represent a barrier to dispersal for one species but not the other. More detailed information on migration and dispersal patterns across these potential geographic barriers in these 2 species may illuminate the link between dispersal and cultural evolution.

We detected little cultural evolution of songs in the 4 sampling sites that were recorded 14–15 years apart, except for the appearance of the song type 3 in the Smithers population in 2011 (Table 3). We could not assess confidently whether there were any shifts in dialect boundaries across our sampling periods because there was not sufficient overlap in the sampling sites (Table 1). It is likely that 15 years is not sufficient time to detect cultural evolution, but a more refined analysis of key acoustical features might reveal slight changes in songs across time. Nevertheless, our study provides an initial basis for comparison in rates of cultural evolution with other birds. In 2 subspecies of the White-crowned Sparrow (*Z. l. pugetensis* and *Z. l. oriantha*), changes in dominant syllable types can be detected in some populations recorded 25–30 years apart (Chilton and Lein 1996a, Harbison et al. 1999, Chilton et al. 2002, Nelson et al. 2004). In Brown-headed Cowbirds (*Molothrus ater*), certain song elements changed over 30 years while other elements remained stable (O’Loughlen et al. 2011, 2013). Other studies have shown that song dialects remained stable for 19 years (Black-capped Chickadee [*Parus atricapillus*]: Ficken and Popp 1995) and 40 years (Medium Ground-Finch [*Geospiza fortis*]: Goodale and Podos 2010). In contrast, changes in song dialects have occurred over only 11 years in the Yellow-naped Amazon (*Amazona auropalliata*), a non-oscine vocal learner (Wright et al. 2008). Continued efforts to resample songs in these species to track long-term changes will provide important insights into variations in the dynamics of cultural change across systems.

We did not formally assess the function of song variation in this study. Playback of conspecific songs to territorial male Golden-crowned Sparrows elicits strong responses (G. Chilton and D. Shizuka personal observations). Thus, songs of Golden-crowned Sparrows seem to function in competition for breeding territories, as they do for all other *Zonotrichia* sparrows (Norment et al. 1998). However, we do not yet know whether males discriminate between potential competitors based on dialect, nor do we know what role songs and song variation play in mate choice. Previous studies on White-crowned Sparrows suggest that there is no assortative mating in mixed-dialect populations (Chilton and Lein 1996c). While there are signatures of reduced gene flow at dialect boundaries in some cases (MacDougall-Shackleton and MacDougall-Shackleton 2001), it is not clear whether song variation is a cause or a correlate of genetic variation. Many of these

patterns could be explored with Golden-crowned Sparrows, and such study could allow for more comparative approaches to understanding the origins and maintenance of geographic variations in bird song.

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Author contributions: D.S. conceived the idea and analyzed the data. D.S. and G.C. performed the field study and wrote the paper. M.R.L. edited the paper and contributed substantial resources and funding.

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Appendix. Recordings provided by Macaulay Library.

Accession Number	Location	Date	Recorder
130847	AK (North Slope)	June 10, 2006	MJ Andersen
130848	AK (North Slope)	June 29, 2006	MJ Andersen
130856	AK (Nome)	June 10, 2006	MJ Andersen
131474	AK (North Slope)	June 10, 2006	G. Vyn
136365	AK (Nome)	June 1, 2007	MJ Andersen
136369	AK (Nome)	June 1, 2007	MJ Andersen
136488	AK (Kenai)	June 29, 2007	MJ Andersen
136493	AK (Kenai)	July 3, 2007	MJ Andersen
136495	AK (Homer)	July 3, 2007	MJ Andersen
136499	AK (Homer)	July 3, 2007	MJ Andersen
137556	AK (Nome)	June 1, 2007	G. Vyn
137589	AK (Nome)	June 4, 2007	G. Vyn