USING SONG DIALECTS TO ASSESS THE MIGRATION STRATEGY OF THE GOLDEN-CROWNED SPARROW

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ABSTRACT: Most techniques used to study migration of wild birds require capture for banding or for attachment and/or recovery of tags or transmitters. We took advantage of the fact that the Golden-crowned Sparrow (*Zonotrichia atricapilla*) sings in winter, combined with published data on the distribution of its distinct song dialects in the breeding range, to assess its migration strategy and migratory connectivity by means of these dialects. Using recordings of the Golden-crowned Sparrow's song across much of its winter range, we categorized these birds by song type to identify their likely origin in some subset of the breeding range. This method allows examination of migration without the need to capture birds. Our results fit best with a pattern of chain migration, with the northernmost breeders wintering in the northernmost part of the winter range, and the southerly breeders wintering farther south. The results suggest strong migratory connectivity between segments of the breeding and winter ranges, though our small sample size makes it difficult to draw firm conclusions on connectivity.

The patterns of migration of long-distance migrants have been traditionally characterized as one of two types—chain migration or leapfrog migration (Berthold 2001, Newton 2008). Chain migration is characterized by the most northerly breeding populations of a species wintering in the most northerly portions of the winter range and the more southerly breeders wintering to the south. In leapfrog migration, the most northerly breeders winter farthest south, leaping over the southern breeders, which winter farther north. While chain migration seems the more straightforward and efficient strategy, leapfrog migration has been confirmed among many species. Swarth (1920), using specimens, is credited as the first to document leapfrog migration of various subspecies within the Sooty (*unalaschcensis*) subspecies group of the Fox Sparrow (*Passerella iliaca*). Since then, leapfrog migration has been demonstrated in many different taxa including numerous species of shorebirds (Salomonsen 1955, Boland 1990, Drent and Piersma 1990, Alves et al. 2012, Duijns et al. 2012), Bulwer's Petrel (*Bulweria bulwerii*; Ramos et al. 2015), Golden Eagle (*Aquila chrysaetos*; Nelson et al. 2015), American Kestrel (*Falco sparverius*; Hobson et al. 2009), Western Yellow Wagtail (*Motacilla flava*; Bell 1996), Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*; Lisovski et al. 2019), and Wilson's Warbler (*Cardellina pusilla*; Kelly et al. 2002). Bredis et al. (2020) examined the migration strategies of 23 transequatorial migrants of the Old World and found leapfrog migration the dominant strategy.

More recent data from techniques such as tagging birds with geolocators have demonstrated that migration is much more variable and nuanced than previously appreciated (McKinnon et al. 2013). For example, many species, especially among those breeding in western North America, undergo a molt migration (Pyle et al. 2009, 2018) in which they move first from the breeding area to an intermediate location to complete molt before continuing to their winter range. Reverse migration (Nilsson and Sjöberg 2016), involving movement in counter-intuitive directions, also occurs frequently. In some species, post-breeding migration is a prolonged affair, with some individuals spending more time in transit than on the winter grounds (Wolfe and Johnson 2015). Satellite tracking of Ferruginous Hawks (*Buteo regalis*) revealed that some populations made enormous post-breeding movements, in some cases resulting in migrations three to four times longer than the distance between breeding and wintering locations (Watson et al. 2018).

Hypotheses to account for the seemingly counterintuitive nature of leapfrog migration fall into three main categories. The “competition hypothesis” (Salomonsen 1955, Pienkowski et al. 1985, Holmgren and Lundberg 1993) proposes that more southerly breeders of some species may simply outcompete the northern breeders on the wintering grounds by virtue of their physical or behavioral attributes or because of their prior occupancy of those areas, forcing the northern breeders to migrate farther to find available winter habitats. The other two hypotheses both assume that winter conditions in the more southerly section of the winter range are superior by virtue of milder winters, and that conditions in the northern breeding range permit those breeders to take advantage of those more favorable southern winter conditions. The “spring predictability hypothesis” (Alerstam and Högstedt 1980) suggests that the more predictable timing of conditions ideal for breeding in the far north allows those breeders to make a more direct, continuous migration north in the spring than the southerly breeders that may be forced to interrupt their spring migration if conditions in their breeding range are not ideal. The “time-allocation hypothesis” (Greenberg 1980) is based on the breeding season being much shorter in the north, forcing those breeders to spend more time on the winter grounds. Spending a longer period in their winter range leads them to benefit from the use of more productive southerly wintering areas. All three hypotheses have their proponents, and the observation of Boland (1990:284) holds true today, “at present, there is no consensus as to why leapfrog migration occurs.”

As we understand the migration strategies used by more species, we may come closer to understanding what drives the adoption of one strategy over the other. In particular, knowing the migration strategies of closely related species that share similar breeding and winter ranges should help to focus on the key factors that determine which strategy is best for which species. Two sparrow taxa, the Gambel’s White-crowned Sparrow and the Sooty Fox Sparrow, migrate in the leapfrog pattern and broadly overlap in range, both breeding in Alaska and western Canada and wintering from southwestern Canada south into northern Mexico (Dunn and Alderfer 2017). Another sparrow, the Golden-crowned (*Z. atricapilla*), also occupies similar ranges and is a congener of the White-crowned Sparrow. Gambel’s White-crowned Sparrows and Golden-crowned Sparrows also overlap broadly in winter habitat and often winter in mixed flocks. Therefore, we decided to investigate the the Golden-crowned Sparrow’s migration strategy, to determine if that species also migrates in the leapfrog pattern or in some variation on that strategy.

We approached this question by taking advantage of Shizuka et al. (2016)

having mapped the song dialects in the Golden-crowned Sparrow's breeding range in detail, plus its tendency to sing through the winter (Kelly 1968). Thus, assuming that wintering Golden-crowned Sparrows sing the same song they sing in their breeding range, we should be able to map the winter ranges of the dialects identified by Shizuka et al. (2016) and assess the extent to which birds breeding in specific subsets of the breeding range winter in specific subsets of the winter range, the concept termed "migratory connectivity." Furthermore, provided that connectivity between breeding and winter locations is strong, the high degree of winter site fidelity of the Golden-crowned Sparrow (Mewaldt and Farner 1957, Seavy et al. 2012, Cormier et al. 2016) should increase the likelihood that wintering birds' song types can be mapped into discrete geographic regions. Understanding migratory connectivity is important if conservation efforts for a migratory species are to be focused on the appropriate area.

METHODS

We used winter song recordings from our own collections, as well as from the Macaulay Library (www.macaulaylibrary.org) and Xeno-canto (www.xeno-canto.org). We only used recordings made from November through February to avoid recordings from birds still in migration. This criterion limited the number of suitable recordings available because, while this species sings frequently in October and March, the frequency of song decreases markedly in winter (Kelly 1968, pers. obs.). Table 1 lists the 38 recordings that met our criteria.

To assign winter songs to the song types identified by Shizuka et al. (2016), we examined spectrograms to assess specific elements or combinations of elements that characterize each song type. Shizuka et al. (2016) found that 90% of all breeding individuals they recorded sang one of five song types. Therefore, we assigned winter songs to one of those five song types. Songs that could not be clearly assigned to one of those five types we designated as "other."

Characteristics Defining Song Types

Typical examples of each of the four major song types we found in our samples are shown in Figure 1. Note that we did not encounter any examples of song type 4 in our set of winter recordings.

Song type 1: All Golden-crowned Sparrow songs start with a descending whistle, but only song type 1 starts with two descending whistles. The second whistle is followed by one or more short whistles at the same pitch as the end of the second descending whistle.

Song type 2: This song type is characterized by two whistles following the descending whistle, the first of which is on the same pitch as the end of the descending whistle, and the second at a lower pitch.

Song type 3: In this song type the descending whistle is followed by a whistle at a pitch lower than the end of the descending whistle, then another whistle at a pitch intermediate between the end of the descending whistle and the first whistle, and then a short trill at the same pitch as the last whistle.

Song type 4: This includes three short whistles all at the same pitch as the end of the descending whistle, followed by a trill at a lower pitch.

Table 1 Recordings of Wintering Golden-crowned Sparrows

Catalog number[a]	Song type	Date	Latitude	Longitude	Recordist
ml281908681	1	21 Nov	49.242	−123.112	Neill Vanhinsberg
ml80124441	1	25 Dec	48.667	−122.325	Shane Sater
ml188444351	1	17 Nov	48.641	−123.448	Jody Wells
xc41864	1	26 Dec	48.578	−122.540	Tayler Brooks
ml212346641	1	28 Feb	48.498	−123.395	Carl Hughes
ml199981081	1	17 Jan	48.498	−123.395	Carl Hughes
ml141633631	1	19 Feb	48.491	−123.394	Daniel Donnecke
xc159804	other	12 Nov	48.386	−123.514	Ian Cruickshank
xc153785	1	9 Nov	48.361	−123.542	Ian Cruickshank
ml127786091	2	23 Nov	45.617	−123.162	Oliver Burton
xc481149-52	2	14 Dec	45.565	−122.698	Thomas Magarian
ml173424721	1	21 Nov	43.396	−123.345	Joseph Mooney
ml40873151	3	22 Nov	39.387	−122.050	Ed Pandolfino
ml283141541	3	24 Nov	39.148	−123.174	Bryan McIntosh
xc662998	2	1 Nov	38.936	−121.332	Ed Pandolfino
xc662999	2	1 Nov	38.884	−121.194	Ed Pandolfino
xc663000	5	6 Dec	38.850	−121.208	Ed Pandolfino
xc65301-03	2	4 Nov	38.570	−121.762	Steve Hampton
xc347901	2	25 Dec	38.569	−121.371	Jim Holmes
ml43500411	2	25 Dec	38.566	−121.381	James Holmes
ml281114321	2	5 Nov	38.464	−122.708	Teresa & Miles Tuffli
ml307879351	2	2 Nov	38.445	−122.816	Bob Hasenick
ml223909621	2	1 Dec	38.430	−122.657	Will Anderson
ml284068211	2	23 Nov	38.247	−122.906	Connor Cochrane
ml218240101	2	7 Nov	38.043	−122.799	Teresa & Miles Tuffli
xc600009	2	2 Nov	37.912	−122.707	Ed Pandolfino
ml310971881	2	16 Feb	37.867	−122.310	Teale Fristoe
ml288643601	2	23 Nov	37.827	−121.203	Steven Hunter
ml293752871	2	18 Dec	37.539	−121.825	Derek Heins
ml193012701	2	13 Dec	37.327	−122.082	V. Langdon-Lassagne
ml192706281	2	11 Dec	37.236	−121.881	Garrett Lau
ml285955441	2	29 Nov	37.170	−121.736	Michelle Thurber
ml300227011	5	20 Jan	36.425	−121.233	Paul Fenwick
xc645157	2	14 Feb	35.555	−121.094	Thomas Graves
ml279251891	5	11 Nov	34.928	−119.908	Anonymous
ml212116621	other	26 Feb	34.818	−119.709	Anonymous
ml133972091	2	8 Jan	34.432	−119.555	John Callender
xc395966	5	13 Dec	34.195	−118.120	Lance Benner

[a] ml, Macaulay Library; xc, Xeno-canto.

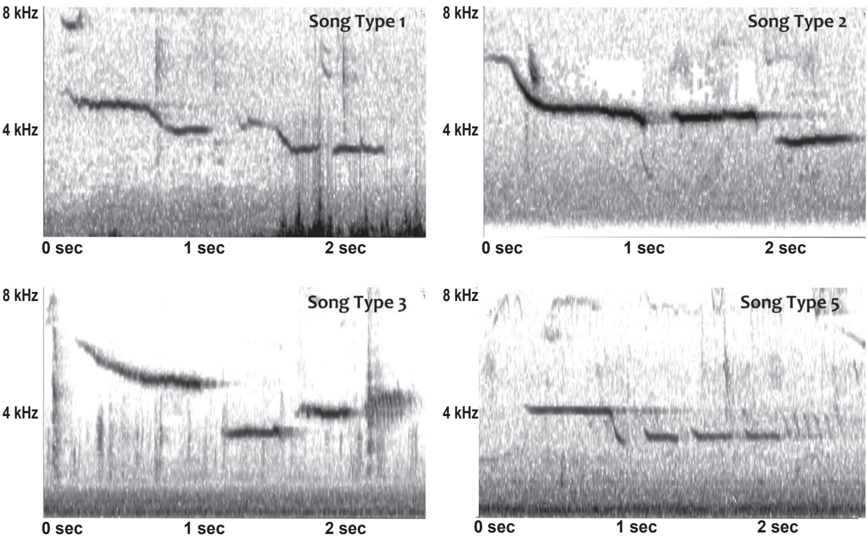

Figure 1. Examples of the four Golden-crowned Sparrow song types (as per Shizuka et al. 2016) in our collection of winter songs. Song type 1 (ml188444351) recorded 17 November in British Columbia by Jody Wells; song type 2 (xc481151) recorded 14 December in Multnomah County, Oregon, by Thomas Magarin; song type 3 (ml40873151) recorded 22 November in Tehama County, California, by Ed Pandolfino; song type 5 (xc663000) recorded 6 December in Placer County, California, by Ed Pandolfino.

Song type 5: This song type is very similar to type 4, except that the ending trill is at the same pitch as the three short whistles.

Distribution of the Song Types in the Breeding Range

Shizuka et al. (2016) found song type 1 only at the extreme northern edge of this species' breeding range, on the Seward Peninsula and in the Brooks Range of northern Alaska. Song type 2 was found along the Gulf of Alaska, while song type 3 was widespread through the eastern and southern parts of the breeding range, from southwestern Yukon Territory south through most of coastal and inland British Columbia. Song type 4 was the rarest of the five major song types identified by Shizuka et al. (2016), recorded principally in inland northern British Columbia. Most recordings of song type 5 were from coastal central British Columbia, with a few from inland northern British Columbia.

RESULTS

The distribution of winter song types we analyzed did not conform to the Golden-crowned Sparrow migrating in a leapfrog pattern (Figure 2). Song type 1 recordings were found only at or near the northern limit of the winter range. Song type 2 was the variation most frequently encountered in

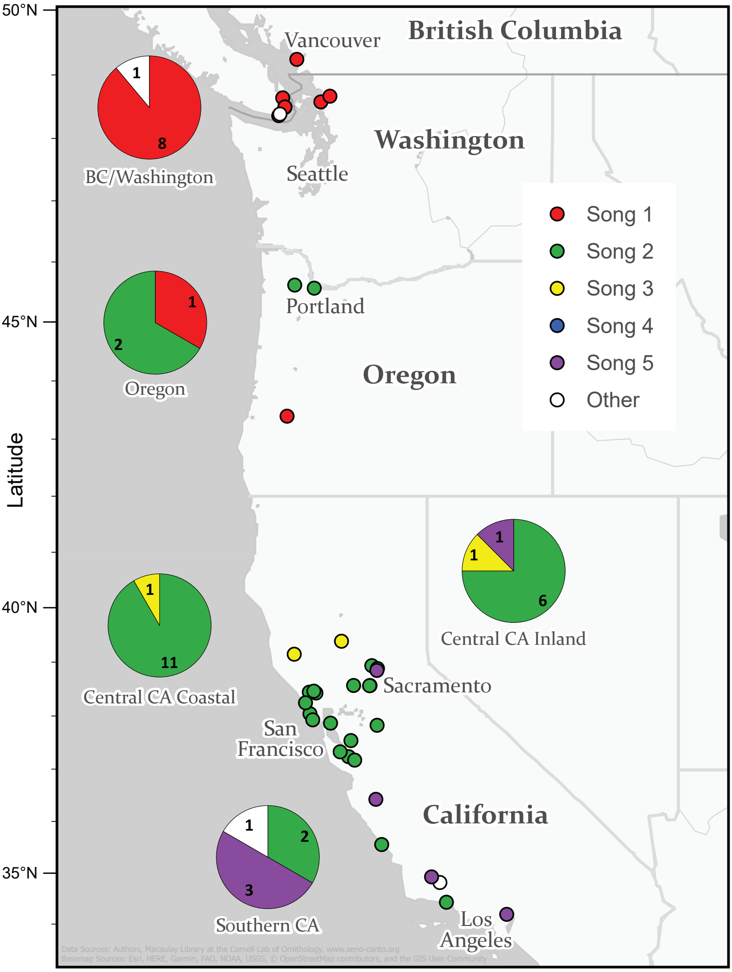

Figure 2. Locations and distribution of various song types (based on Shizuka et al. 2016) of the Golden-crowned Sparrow recorded in winter.

winter, with examples from northern Oregon to southern California. Nearly all the songs recorded in the San Francisco Bay area and central California were of type 2. We identified only two recordings as song type 3, both from north-central California. Of the four recordings of song type 5, three were from southern California.

These winter song recordings show a pattern generally consistent with chain migration. The song type of the most northerly breeders (type 1) was found only in the northern part of the winter range, while song type 5, which Shizuka et al. (2016) found mainly in the southern portions of the breeding range, occurred only in the southern parts of the winter range. We obtained no recordings of song type 4. The preponderance of song type 2 in our sample is likely a reflection of those Gulf of Alaska breeders being common in central California in winter, combined with the high concentration of birders and birding effort in the greater San Francisco Bay area, plus the Golden-crowned Sparrow's relatively high abundance in those same areas.

The two song types we encountered most frequently (1 and 2), showed some geographic clustering. Eight of the nine winter recordings of song type 1 were from extreme southwestern British Columbia or northwestern Washington, and 17 of the 21 examples of song type 2 were from central California, between latitudes 37.2° and 38.9° N.

DISCUSSION

Despite the small sample size, our results appear to rule out leapfrog migration as a general strategy for the Golden-crowned Sparrow. The two song types Shizuka et al. (2016) found most geographically concentrated within the breeding range (1 and 2) both showed a winter pattern best associated with chain migration. That is, song type 1 (birds breeding in northern and northwestern Alaska) was encountered mainly in the northernmost part of the winter range, whereas song type 2 (birds breeding around the Gulf of Alaska) was concentrated in the central part of the winter range.

Our findings are consistent with data from geolocator-tagged birds (Seavy et al 2012, Cormier et al. 2016). These authors tagged wintering Golden-crowned Sparrows near Bolinas north of San Francisco (Marin County) and in inland central California (Placer County). Because those two locations are at similar latitudes, the results of their work do not shed light on this species' migration strategy, though they do allow us to test the consistency of our findings with these independent data. We obtained winter song recordings from the same general locations of those authors' study. Birds from north of San Francisco sang songs of type 2, and the geolocator data showed those birds breeding around the Gulf of Alaska (Seavy et al. 2012), where that song type is expected. Birds we recorded in inland central California sang songs of types 2, 3, or 5. Geolocator data from Cormier et al. (2016) showed most of their birds that wintered in inland central California were breeding in southern Yukon or northern inland British Columbia, where song types 3, 4, and 5 are expected. However, one of those tagged birds bred near the Gulf of Alaska, where song type 2 predominates. The fact that we did not encounter more examples of song type 3 in inland central California may be due to the sampling by Cormier et al. (2016) being highly localized. These authors tagged birds at a single location in the Sierra Nevada foothills near the eastern edge of the species' winter range. This could also reflect that at this scale song types do not allow reliable assessment of location of breeding. Many more samples of winter song are needed to clarify the winter ranges of each dialect population at a finer scale.

Seavy et al. (2012) and Cormier et al. (2016) found a strong degree of migratory connectivity between breeding and wintering locations for the birds at their two sampling locations. Our results appear generally consistent with their observations, at least for birds singing songs of types 1 and 2, in that we found the preponderance of recordings of those birds in relatively discrete winter locations. We did not find enough examples of the other song types to draw any conclusions about migratory connectivity for those dialect populations.

It is particularly interesting that Lisovski et al. (2019) found that the Gambel's White-crowned Sparrow, a close relative of the Golden-crowned Sparrow and a taxon that shares overlapping breeding and winter ranges and similar habitat preferences, migrates in the leapfrog pattern. However, their data are not conclusive. They used a combination of banding, stable-isotope, and geolocator data and found that only the stable-isotope data suggested leapfrog migration. The banding data were compromised by having only three individuals with clear breeding date recoveries. All four of their geolocator-tagged birds wintered at a single site in central California. Of those four, two bred in southwestern Alaska and the other two in northeastern Alaska. Data from more birds of this taxon tagged from a wider range of latitudes could confirm their use of leapfrog migration. This would offer an intriguing basis for speculation about why these taxa use different migration strategies.

The evidence for leapfrog migration in the Sooty Fox Sparrow subspecies is more compelling (Swarth 1920, Bell 1997), though geolocator data from a small sample of birds representing a subset of such sparrows did not corroborate it (Fraser et al. 2018). The winter ranges of this segment of the Fox Sparrow and the Golden-crowned Sparrow are nearly identical. However, the breeding ranges differ substantially. The Sooty Fox Sparrows breed along the coasts of southern Alaska and British Columbia, all areas of relatively wet, mild climate. The Golden-crowned Sparrow's breeding range extends well north and east of this and encompasses a much wider range of climate and habitat types (Norment et al. 1998). Its winter behavior and habitat preferences are also different, with the Fox Sparrow tending to be solitary in winter and found in shady areas with dense understory (Weckstein et al. 2002). Golden-crowned Sparrows are gregarious in winter and use a variety of more open, brushy habitats (Norment et al. 1998, pers. obs.). Bell (1997) concluded that leapfrog migration in these Fox Sparrow subspecies could be explained by ideal winter conditions occurring later in the season in California, causing the early-breeding southern populations to truncate their southward migration but allowing the later-breeding northern birds to continue south to the most favorable locations. It seems that those same reasons should drive the Golden-crowned Sparrow to adopt a similar leapfrog migration, but our results are not consistent with that. Perhaps the contrasting winter habitat preference of the Golden-crowned Sparrow is responsible for the difference in migration strategy. In any case, a direct comparison with the Gambel's White-crowned Sparrow, should that species be confirmed as a leapfrog migrant, would provide a much better basis for assessing factors resulting in a different type of migration strategy.

Our use of winter song dialects to assess migration strategy offers some advantages over other methods. It does not require the capture or recapture of birds and can benefit from the rapidly increasing number of recordings being archived. It does require that the breeding-season dialects be discernable, documented, and well-mapped, and that the species sings in winter. Indeed, DeWolfe and Baptista (1995) used this method to investigate migration of the Puget Sound White-crowned Sparrow (*Z. l. pugetensis*). They found that wintering flocks were composed of birds singing various dialects, and this subspecies did not appear to demonstrate leapfrog migration.

DeWolfe et al. (1974) and Nelson (1998) both examined variation in songs of the Gambel's White-crowned Sparrow at a few locations and found little evidence of regional dialects. Subsequently, Chilton et al. (2002) reviewed songs of this sparrow over a much broader range and did find distinct regional dialects. There are numerous recordings of Gambel's White-crowned Sparrow song throughout its winter range. Therefore, application of this song-dialect approach to the Gambel's White-crowned Sparrow, if it confirms leapfrog migration in this subspecies, may yield important clues about the basis for selection of different migration strategies by these two *Zonotrichia* sparrows.

Wider implementation of this approach, of song dialects as a tool to study bird migration on a broader scale and for more species, is dependent on access to more recordings, from all seasons. With more and more access to recording devices (even a smart phone can work well), the potential for community science to make important contributions grows. Archives such as the Macaulay Library (www.macaulaylibrary.org), which maintains all recordings uploaded to www.eBird.org, and Xeno-canto (www.xeno-canto.org), make it easy to upload and access recordings. We encourage everyone to record and upload recordings of bird vocalizations as often as possible.

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