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Avian Behavior, Ecology, and Evolution

The influence of migratory routes, breeding, and wintering grounds on cultural shifts in song of White-throated Sparrows (*Zonotrichia albicollis*)

La influencia de las rutas migratorias, las zonas de cría y de invernada sobre los cambios culturales del canto del Gorrión Garganta Blanca (*Zonotrichia albicollis*)

Joel A. Khoo[1], *Amelia J. MacDonald*[2], *Ingebjorg Jean K. Hansen*[3], *Cody M. Cox*[4], *Scott M. Ramsay*[5] and *Ken A. Otter*[1]

ABSTRACT. For song variants to spread among widely separated breeding populations by cultural evolution, song sharing would have to occur in locations where birds physically overlap in time and space, such as common wintering grounds and/or migratory routes. To identify such spatiotemporal links between populations, we used the Motus Wildlife Tracking System to investigate whether White-throated Sparrows (*Zonotrichia albicollis*) in three disparate breeding populations in British Columbia migrate to common wintering grounds and overlap on migration pathways. We also tracked sparrows overwintering in a single eastern region (Georgia, United States) to determine whether they disperse to multiple breeding regions. Except for a single sparrow that migrated to California, all other sparrows tagged on western breeding grounds (N = 23) were either detected in, or converging on, the south-central United States. Further, we detected a common migratory pathway tracking the southern edge of the boreal forests in Canada and the western edge of the Eastern Temperate Forests in the United States. This migratory route coincides with regions where previous studies have shown the rapid spread of novel song variants (doublet-ending songs) over short time scales; birds share not only a common wintering ground, but also a common migratory pathway that might reinforce song sharing if song learning extends into the bird's first spring. Along with learning biases, this could explain the rapid, widespread adoption of novel song variants within the past two decades across western and central Canada. We confirmed that birds from a single wintering location in Georgia dispersed across a wide region during northward migration, which also corresponds to locations where other song variants (triplet-ending) have persisted.

RESUMEN. Para que las variantes de canto se propaguen entre poblaciones reproductoras ampliamente separadas mediante evolución cultural, el intercambio de cantos debería ocurrir en lugares donde las aves se superpongan físicamente en tiempo y espacio, como zonas de invernada comunes y/o rutas migratorias. Para identificar tales vínculos espacio-temporales entre poblaciones, utilizamos el Sistema de Seguimiento de Vida Silvestre Motus para investigar si los gorriones de garganta blanca (*Zonotrichia albicollis*) de tres poblaciones reproductoras distintas en Columbia Británica migran hacia zonas de invernada comunes y se superponen en las rutas migratorias. También rastreamos gorriones que invernaban en una única región del este (Georgia, Estados Unidos) para determinar si se dispersan a múltiples regiones de cría. Excepto por un solo gorrión que migró a California, todos los demás gorriones marcados en las zonas de reproducción occidentales (N = 23) fueron detectados en el centro-sur de los Estados Unidos, o se dirigían hacia ahí. Además, detectamos una ruta migratoria común que sigue el límite sur de los bosques boreales en Canadá y el límite occidental de los Bosques Templados del Este en los Estados Unidos. Esta ruta migratoria coincide con regiones donde estudios previos han demostrado una rápida propagación de variantes novedosas de cantos (cantos de final doble) en escalas de tiempo cortas; las aves no solo comparten una zona de invernada común, sino también una ruta migratoria común que podría reforzar el intercambio de cantos si el aprendizaje del canto se extiende hasta la primera primavera del ave. Junto con los sesgos de aprendizaje, esto podría explicar la adopción rápida y generalizada de variantes novedosas de cantos en las últimas dos décadas en el oeste y centro de Canadá. Confirmamos que las aves provenientes de un único lugar de invernada en Georgia se dispersaron por una amplia región durante la migración hacia el norte, lo cual también corresponde a zonas donde otras variantes de cantos (cantos de final triple) han persistido.

Key Words: *migration; shared wintering and breeding grounds; song cultural shifts; song learning*

INTRODUCTION

Geographic song variation in songbirds, where individuals within a geographic area share common song features or song types, and which differ from those in other regions, arise through song-learning in passerines (DeWolfe and Baptista 1995, Nordby et al. 2002). Whereas some songbird species can continue to acquire new song variants into adulthood (open-ended learners), other species appear to acquire songs as juveniles to early adulthood (closed-ended learners); these songs crystallize and thereafter may change little for the rest of their lives (Brenowitz and Beecher 2005). Among species on the closed-ended learners end of the spectrum, juvenile songbirds typically acquire songs from conspecific tutors within their first year of life; this can start from males encountered prior to their first migration (Marler 1970) but social interactions with tutors on migration, wintering grounds, or even first breeding grounds can also influence which song

[1]Department of Ecosystem Science & Management, University of Northern British Columbia, Canada, [2]Birds Canada, Delta, BC, Canada, [3]Ministry of Water, Land and Resource Stewardship, Dawson Creek, BC, Canada, [4]Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, United States, [5]Department of Biology, Wilfrid Laurier University, Waterloo, Ontario, Canada

variant males sing (Baptista and Petrinovich 1984, Petrinovich and Baptista 1987, Nordby et al. 2001, Nulty et al. 2010, Mennill et al. 2018). During such song-acquisition interactions, juveniles may even learn more note variants than are generally found in the repertoire they sing as adults (termed overproduction) and refine these upon settling on their first breeding territory to match the songs sung by others in their local neighborhood (Nelson 2000). This "selective attrition" (Nelson 2000) and choice of local tutors helps reinforce the establishment of geographic song variants, as conformist biases (Lachlan et al. 2018) can result in common song variants to rise in frequency at the expense of rarer variants. However, recent work has shown that vocal variants can spread rapidly across large geographic regions through cultural evolution even when those variants are initially rare (Garland et al. 2015, 2017, Otter et al. 2020), which suggests that chosen tutors may not always be constrained to those sharing songs common on natal breeding areas. One mechanism for the sharing of vocal variants among geographically isolated breeding populations is the selection of tutors during other periods of the annual migration cycle, such as acquiring song variants from tutors encountered in wintering areas (Otter et al. 2020, Chartier et al. 2022). This suggests that some closed-ended learners may adopt learning biases other than the conformist approach (Lachlan et al. 2018), and exposure to tutors from different populations could allow novel song variants to be acquired and spread widely across disparate breeding regions (Garland and McGregor 2020).

Several other learning biases have been proposed that may influence the acquisition of novel song variants among juvenile birds (Byers et al. 2010). A model-based learning bias suggests juveniles learn song-types based on the phenotypic characteristics of different tutors they encounter, preferentially mimicking songs of either the most dominant or successful males (Byers et al. 2010). In contrast, content-based bias suggests that preferential learning or selection for a song is due to its acoustic structure (Byers et al. 2010). Taken together, juvenile birds encountering either dominant males or hearing songs with a particular acoustic structure on shared wintering grounds might bias the acquisition of these song variants, which begins to explain how cultural spread of song occurs within and among populations (Byers et al. 2010, Otter et al. 2020, Williams and Lachlan 2021).

Our work has focused on the rapid cultural spread of songs among widely separated breeding populations of the White-throated Sparrow (*Zonotrichia albicollis*) across the continental scale of North America. White-throated Sparrows breed across most of Canada and parts of the northeastern United States, spanning approximately 5000 km from British Columbia and the Yukon in the west to Newfoundland on the Atlantic coast (Falls and Kopachena 2020). Males are highly vocal and easily recorded, and the exponential growth of sound libraries for citizen scientists to deposit songs creates the opportunity to address how cultural evolution of song occurs at continental scales in this species. Individual male White-throated Sparrows typically sing a single song variant that does not change markedly between years, placing them on the closed-ended end of Brenowitz and Beecher's (2005) song-learning spectrum. Male song comprises multiple, whistled introductory notes, which typically either descend or ascend in frequency between each sequential note (Borror and Gunn 1965, Ramsay and Otter 2015). This introductory phrase is followed by series of repeated terminal notes (the terminal strophe), which normally consist of three (triplet) or two (doublet) notes at a single frequency and cadence, which is repeated a variable number of times (Borror and Gunn 1965, Ramsay and Otter 2015). The introductory phrase shows high variability in structure within populations (Borror and Gunn 1965) but there is little evidence that males within single breeding populations adopt common introductory phrase structure (i.e., no evidence for general conformity in the introductory phrase; Lemon and Harris 1974). The opposite, though, is true of the terminal strophes. The traditional terminal strophe is a triplet of notes (Borror and Gunn 1965) that was nearly ubiquitous across the entire breeding range of the species in the 1950s/1960s. Song is commonly heard from this species throughout the breeding season (late April through July), but songs are frequently recorded on wintering grounds occupied between October to March as evident by songs deposited on sound recording libraries from these regions (Otter et al. 2020). Further, song activity (based on temporal patterning of deposited sound recording) begins to increase on wintering grounds during January through March, which geolocator studies reveal is prior to birds departing on northward migrations (Otter et al. 2020). Song recordings are also reported all along migratory corridors during late April/early May, which corresponds to the period of northward migration (Otter et al. 2020). These observations suggest sparrows may be exposed to songs not only in natal breeding areas, but also on wintering grounds and migration routes.

Our studies have documented continent-wide spreads of doublet-ending song variants over the past 20–25 years (Otter et al. 2020, Chartier 2021), suggesting that the terminal strophes of the song undergo cultural evolution both within (Ramsay and Otter 2015, Zimmerman et al. 2016, Chartier et al. 2022) and between populations (Otter et al. 2020, Chartier 2021). Further, novel song variants, such as a modulated version of the doublet-ending song, periodically emerge and rapidly spread both within (Chartier et al. 2022) and between populations (Chartier 2021), despite being initially rare. This could be facilitated if individuals from disparate breeding populations have periods of spatiotemporal overlap with tutors from other populations. This, coupled with model-based or content-based learning biases, would allow novel song variants to rapidly spread to different geographic regions, as has been shown in instances of cultural spread of vocal signals in other groups, such as whales (Garland et al. 2015, 2017). Yet, despite the extensive spread of the doublet-ending song variants across much of western and central Canada in the past 20 years, breeding populations in the eastern, Atlantic provinces of Canada have still largely maintained the triplet-ending song variants (Otter et al. 2020, Chartier 2021). This persistence of the triplet-ending variant suggests that there might be some limitations in spatiotemporal overlap of birds that reduce the spread of song variants to some regions.

Otter et al. (2020) used geolocators to demonstrate that White-throated Sparrows from one western population overwintered in an area of the south-central United States that is the suspected wintering grounds of White-throated Sparrows from central Canada (Mazerolle et al. 2005). This showed the potential of sparrows breeding in widely disparate locations in Canada's boreal forests to overlap on common wintering grounds with

tutors from other populations for approximately half of their initial, song-learning year. However, the extent that geographically isolated breeding populations share common migratory pathways and converge on common over-wintering sites in this species has not been fully explored. The Motus Wildlife Tracking System (Motus; Taylor et al. 2017) provides the potential to investigate whether sparrows intermix during migration between breeding and wintering grounds, as has been seen in other species (Knight et al. 2018).

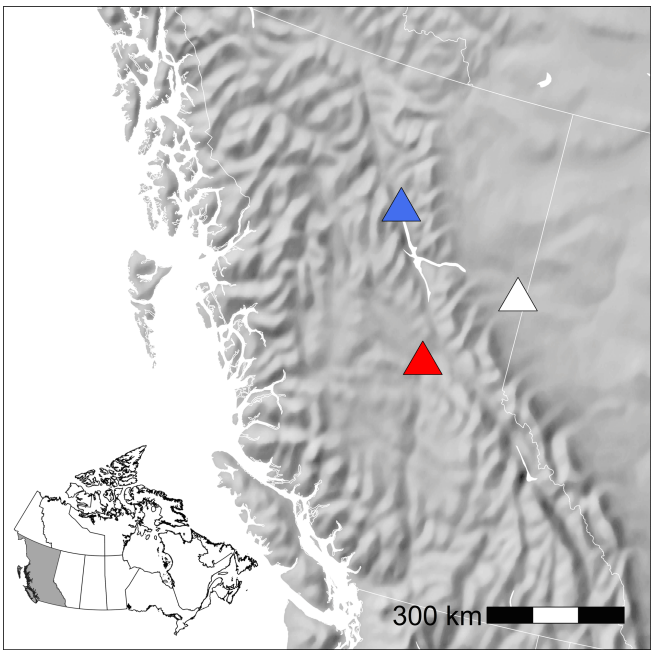
Our objective was to use Motus to evaluate if some individuals in disparate breeding populations of White-throated Sparrows in British Columbia migrate to common wintering grounds along overlapping migration routes, thus facilitating the potential cultural transmission of song variants. We also investigated if populations on opposite sides of the Rocky Mountains display bifurcate migratory pathways, with some birds migrating east to overwintering areas in the south-central parts of the United States, and others converging on the smaller, isolated population of birds overwintering along the Pacific coast of the western United States (Falls and Kopachena 2020). Finally, to shed light on why the breeding populations in the Atlantic provinces of Canada have largely retained the triplet-ending song variants, we incorporated Motus data from White-throated Sparrows tagged on the wintering grounds in the southeastern United States. This allowed us to test whether the Atlantic breeding populations have distinct migration pathways from the western (Manitoba to British Columbia) and central (Ontario and Québec) breeding populations, which would limit the potential for cultural song exchange among these populations.

METHODS

Study area

Our study sites included three disparate breeding populations of White-throated Sparrows in British Columbia (Fig. 1). Between 15 May and 31 May 2022, 50 males were tagged in Prince George (n = 25: 53.84°N, -122.76°W) and Dawson Creek (n = 25: 55.72° N, -120.49°W) on opposing sides of the Rocky Mountains in central and northeastern British Columbia, Canada. An additional 18 males were tagged in Tsay Keh Dene (56.94° N, -124.96°W), west of the Rocky Mountains but several hundred km north of Prince George, British Columbia, between 6 June and 11 June 2023. All three breeding populations are separated by at least 240 km, are climatically distinct, and occur in different biogeoclimatic zones and subzones. The Dawson Creek and Tsay Keh Dene capture locations were both in the Boreal White and Black Spruce biogeoclimatic zone, but different subzones with Tsay Keh Dene being cooler and drier on average (Meidinger and Pojar 1991). The mixed-wood forests found there are predominantly white spruce (*Picea glauca*) or black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloides*) with minor components of balsam poplar (*Populus balsamifera balsamifera*). The Prince George capture site was in the Sub-Boreal Spruce biogeoclimatic zone, where forests are primarily coniferous and dominated by hybrid spruce (*Picea glauca x engelmannii*), lodgepole pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*) or Douglas-fir (*Pseudotsuga menziesii*), with localized deciduous and mixed forests containing trembling aspen and black cottonwood (*Populus balsamifera trichocarpa*).

Fig. 1. Relative locations of tagging sites in Dawson Creek (white), Prince George (red), and Tsay Keh Dene (blue). The map was made using QGIS (QGIS Development Team 2022).



To expand our study, we also partnered with another research team deploying Motus tags on a wintering population of White-throated Sparrows east of the Appalachian Mountains (Georgia). Our banding objective had been to determine whether sparrows from discreet breeding populations converged upon common wintering areas; by partnering with colleagues in Georgia, we were able to determine whether birds occupying a common wintering region dispersed to multiple breeding regions. In addition, this represented a wintering area on the east coast of the United States, much farther east than previous studies have found for birds that breed in western Canada (Otter et al. 2020); this would help elucidate whether different song variants are maintained on breeding grounds through breeding populations being occupied by birds on different wintering grounds. Twenty-four White-throated Sparrows were tagged on the wintering grounds near Athens, Georgia (33.90°N, -83.38°W), between 24 January and 15 April 2023, and 7 were tagged between 3 December 2023 and 16 March 2024.

Field methods

Breeding territories of White-throated Sparrows within each population were located using song playbacks and males were captured in mist nets with song playbacks and a plastic decoy as lures. We individually fitted sparrows with VHF (very high frequency) radio-transmitters (Lotek© NTQB2-3-2-M NanoTags) using a figure-8 leg-loop harness design modified from Rappole and Tipton (1991). The harness was made of 0.7mm Stretch Magic® elastic thread sealed using crimp beads and superglue. Together with the transmitter, the apparatus weighed 0.9 g which was 3.5% of the average weight of sparrows in this study (26 ±1.1SD g). The radio-transmitters had a burst interval of 34.9

seconds in Prince George and Dawson Creek in 2022, and 29.3 seconds in Tsay Keh Dene in 2023 and transmitted at 166.38 MHz. This provided an estimated battery life of 402 and 368 days in 2022 and 2023, respectively. During tagging, we used a handheld radio receiver (Communications Specialists Inc. R1000, Lotek SRX600 or SRX1200), to ensure that tags were functioning before sparrows were released. In spring 2023 and summer 2024, we surveyed known territories of previously tagged males to remove transmitters where possible. All research was carried out according to the guidelines prescribed by the Canadian Council on Animal Care and approved by the Animal Care and Use Committee of the University of Northern British Columbia (Protocol 2020-04 & 2023-15).

Wintering White-throated Sparrows were captured in passive mist nets at three sites in Clarke County, Georgia in the winters of 2022–2023 and 2023–2024. All individuals received uniquely numbered USGS-issued aluminum bands and unique combinations of three plastic color bands to aid in individual identification. Individuals weighing at least 27 g were fit with VHF radio transmitters (Lotek© NTQB2-4-2S-M) using figure-8 leg loop harnesses constructed using 0.7mm Stretch Magic® elastic thread secured with crimp beads and superglue. The combined transmitters and harnesses weighed 1.1 g, which was no more than 4% of the body mass of tagged individuals, in accordance with federal permits. The transmitters had a burst interval of 38.9 seconds, resulting in an estimated battery life of 846 days, and transmitted at 166.38 MHz. We used a handheld radio receiver (Lotek Biotracker) to ensure that tags were functioning before releasing tagged individuals. Individuals that did not meet the 27 g weight threshold were not tagged, in accordance with federal permits. All research in Georgia was conducted under U.S. federal bird banding permits issued by the United States Geological Survey (USGS) Bird Banding Laboratory (permit #24181) and with the approval of the University of Georgia Institutional Animal Care and Use Committee (Protocol A2022 08-004-Y3-A0).

Data processing and analysis

Mapping

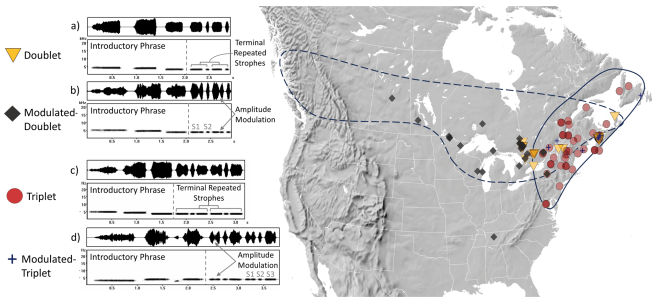
We downloaded detection data from the centralized Motus database for the 99 radio-transmitters we deployed on White-throated Sparrows. Because of radio interference, Motus detection data typically include some false positive detections. We used an automated filter to categorize detections with three or fewer consecutive hits of the same radio-transmitter (runs) or detections with four consecutive hits in noisy environments (≥ 100 detections within an hour and ≥ 85% of detections with run length ≤ 2 hits) as likely false (Birds Canada 2024). We then calculated the proportion of detections that were categorized as likely false for each combination of radio-transmitter, Motus station, and day, and removed all detections where the proportion was > 0.5. This additional step helped to exclude spurious data from Motus stations with particularly high levels of radio interference. We then created a route map and plot of signal strength of the detections for each bird and examined them individually. We excluded detections that met one or more of the following criteria that suggested a false positive: (1) a large movement at an impossible flight speed (> 72 m/s); (2) a large movement in a direction that did not match known migration routes and no curve pattern in detection signal strength (dB) that was indicative of a bird flying through a receiver antenna beam (Birds Canada 2024); or (3) an isolated detection (no detections on other nearby receivers) with a relatively short run length (< 10 hits) and no clear detection curve pattern.

To process and map Motus data, we used R Statistical Software (R Core Team 2023), RStudio (Posit Team 2023), and the following packages: DBI (Wickham and Müller 2022), ggmap (Kahle and Wickham 2013), lubridate (Grolemund and Wickham 2011), motus (Birds Canada 2024), rnaturalearth (Massicotte and South 2023), sf (Pebesma 2018), tidyverse (Wickham et al. 2019), and viridis (Garnier et al. 2023).

Song analysis

We compared the migratory pathways of western birds with known locations of the doublet-ending and modulated-doublet song variants known from previous studies (Otter et al. 2020, Chartier 2021, Chartier et al. 2022; see Fig. 2), as well as locations of these song variants posted to the Macaulay Library of Sound (Cornell University Laboratory of Ornithology) during May to July in 2022 and 2023 (Fig. 2). Similarly, we compared Georgia-wintering birds with locations of triplet-ending song variants posted to the Macaulay Library of Sound during 2022 and 2023 (Fig. 2). Recent studies have shown that the triplet-ending song variant is increasingly isolated to the far eastern portion of the White-throated Sparrow range (Otter et al. 2020, Chartier 2021; Fig. 2), so a secondary objective was to determine if eastern wintering birds use a separate migratory pathway. For all songs included in Figure 2, only recordings with high signal-to-noise ratios were included for inspection of song types. This ensured that the songs used for classification were recorded at close distances, so patterns of song structure were less likely to be biased by vegetational reflectance or wind disturbance, and notes could be clearly delineated. Further, songs were only classified if there was a minimum of two repeating strophes in the terminal phrases, so to reduce ambiguity of the repeating pattern of notes (Ramsay and Otter 2015). We used the spectrographic features on the Macaulay Library of Sound to visually inspect each song, categorizing these as triplet-ending if the terminal strophes consisted of a repeating three-note pattern typical of the traditional pattern noted by Borror and Gunn (1965). During this analysis, though, we detected a possible emergence of a new song variant: a modulated triplet, where the first note of the triplet-ending strophe had a similar pronounced amplitude modulation to the modulated-doublet described by Chartier et al. (2022). For several of the situations where modulated notes were suspected from audio and visual inspection, we contacted recordists to request sound files and confirmed amplitude drops/rises in the first note matching the 50% amplitude drop used to categorize the modulated-doublet (Chartier et al. 2022). Of 72 triplet-ending songs analyzed from these two years, 60 were classified as unmodulated triplet-ending, whereas only 12 were modulated-triplets (Fig. 2). For the purposes of this study, though, we focused primarily on whether migratory divides separate populations using triplet-ending or doublet-ending song variants; the potential extent of spread of a new eastern song variant (the modulated-triplet) is an avenue for future investigation.

Fig. 2. The current distribution of doublet-ending song variants (inclusive of both unmodulated variants described in Ramsay and Otter 2015, and modulated-doublets described by Chartier 2021 and Chartier et al. 2022) in the White-throated Sparrow (*Zonotrichia albicollis*) breeding range is indicated by the dashed outline. That of triplet-ending songs (including the traditional triplet-ending song described by Borror & Gunn 1965, as well as a modulated-triplet variant described here for the first time) is shown by the solid outline. In the inset to the left are spectrograms/waveforms showing the distinction between the four song variants, highlighting differences in the number of repeating notes in the terminal strophes, as well as amplitude modulations in the S1 note that characterize the modulated song variants. Songs deposited into the Macaulay Library of Sound during 2022 and 2023 were classified to ending variant, and are superimposed on the map as points, represented as inverted triangles (unmodulated doublet-ending), diamonds (modulated-doublet ending), circles (unmodulated triplet-ending), or crosses (modulated-triplet ending). Only songs that could be clearly delineated from online spectrograms (representing high signal-to-noise ratio recordings) as clearly modulated or not, and clearly doublet-ending or triplet-ending were included. Exemplar recordings used for waveform/spectrograms in the figure were from personal recordings (doublet and modulated doublet) or recorded by George Forsyth (unmodulated-triplet - ML587953921) and Laura Sebastianelli (modulated-Triplet - ML581684431).



RESULTS

Migratory direction of western breeding populations

After filtering, 38 of the initial 68 tagged White-throated Sparrows (56%) were detected by at least one Motus station, but 14 of these were only detected at the station closest to their banding site or a station close to their banding site, so no information was available for determining migratory pathways or wintering grounds. A total of 24 individuals were detected at a sufficient number of Motus stations to determine either routes used and/or wintering grounds; this included sparrows from Prince George (n = 10), Dawson Creek (n = 7), and Tsay Keh Dene (n = 7). Based on detections in fall 2022, spring 2023, fall 2023, and spring 2024, 16 of the 24 birds (67%) could be tracked to wintering locations; only one tagged bird from the Prince George breeding population was observed migrating to California (Figure 3A); all 15 of the remaining birds combined from Prince George, Dawson Creek, and Tsay Keh Dene migrated southeast and were detected at stations in Iowa, Kansas, and Missouri in the United States. The remaining 8 birds all displayed eastward migratory direction, but none were detected further south than central Minnesota, United States. Connecting the paths of eastward movement suggested that birds moved along the southern edge of the Canadian boreal forest from British Columbia to southern Manitoba, and along the interface of the Great Plains - Eastern Temperate Forests ecotone in the United States (United States Environmental Protection Agency 2023; Fig.3A).

Sparrows from Prince George (n = 1) and Dawson Creek (n = 4) were detected on return migration pathways in spring 2023, and sparrows from Tsay Keh Dene (n = 3) were detected on migration in spring 2024. The individual that returned to Prince George was the only sparrow for which two fall migrations were observed. All return routes followed similar pathways as those depicted for fall migration in Figure 3A. These routes are spatially aligned with geographic spread of the doublet-ending and modulated-doublet ending song variants over the past 20 years (Otter et al. 2020, Chartier 2021).

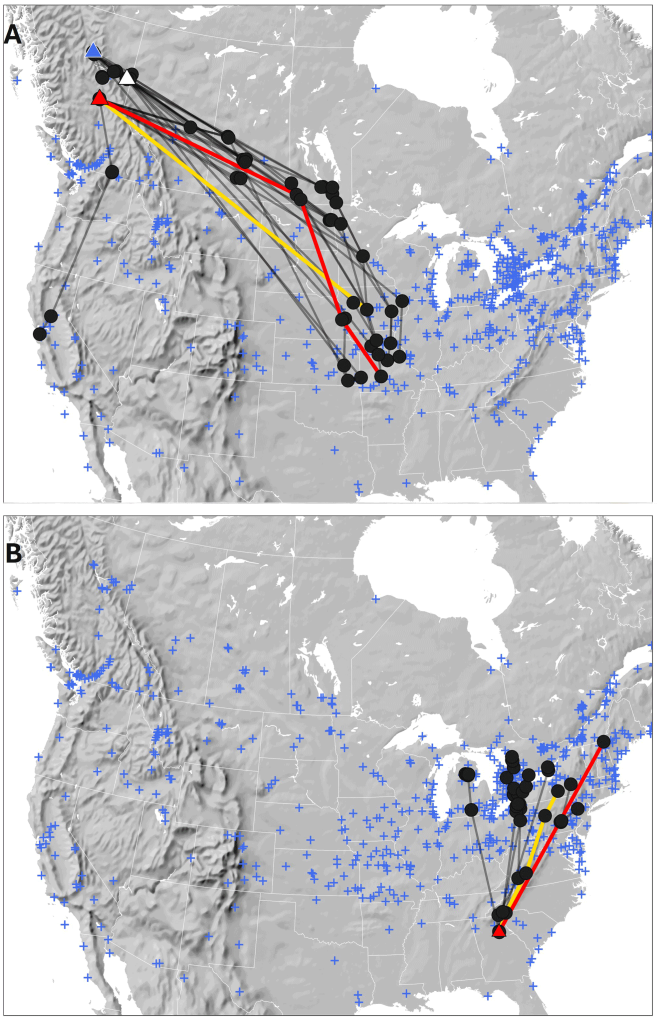
Migratory direction of eastern populations

Of the 31 White-throated Sparrows tagged in Georgia, 19 were detected by at least one Motus station (61%), but only 11 were detected at three or more stations from which migratory direction could be determined (Fig. 3B). Based on detections in spring 2023, fall 2023, and spring 2024, 8 sparrows were detected at stations on the breeding grounds, with the majority converging on southeast Ontario and east of the Great Lakes. The remaining 3 were detected on route and displayed a north-northeast migratory direction. One sparrow was observed in both spring migratory periods (Fig. 3B).

DISCUSSION

Among White-throated Sparrows breeding in northern British Columbia, we detected two distinct migratory pathways, though one route was substantially more prevalent among individuals included in our study. Although one individual from Prince George, British Columbia was detected over-wintering on the Pacific coast of northwestern California, the remaining White-throated Sparrows we tracked beyond their breeding grounds used a common migratory path across the southern edge of the Canadian boreal forest to converge on wintering grounds in the south-central United States. For birds tagged in Prince George and Tsay Keh Dene, this entailed crossing the Rocky Mountains on migration and converging with birds that bred across the Canadian Prairies. Our results mirror findings of geolocator studies, which revealed a similar proportion of sparrows from Prince George migrating to California and the south-central United States (Otter et al. 2020). However, the sample size in the current study was much higher and included three geographically separated populations of birds in northern and central British Columbia on either side of the Rocky Mountains instead of the single population in the previous study. This confirms that birds from multiple breeding locations converge on common wintering grounds, which would increase the potential of individuals to encounter tutors from other breeding populations and facilitate the cultural spread of song-variants spread among populations.

Fig. 3. (A) Fall migratory movements of White-throated Sparrows (*Zonotrichia albicollis*) tagged on western breeding grounds in 2022 and 2023. White, red, and blue triangles correspond to sparrows tagged in Dawson Creek, Prince George, and Tsay Keh Dene, British Columbia, Canada, respectively. (B) Spring migratory movements of White-throated Sparrows tagged in an eastern wintering ground (red triangle; near Athens, Georgia) in 2023 and 2024, showing that birds from a common wintering ground disperse toward a broad array of breeding grounds in southeastern Ontario, Quebec, and Atlantic United States/Canada. Black circles represent detections at Motus receivers; black lines connecting receivers represent sequential detections for individuals rather than actual migratory routes. Blue crosses indicate locations of active Motus receivers during the study period. A single individual was observed during the fall migratory periods of both 2022 and 2023 (A), and another in the spring migration in 2023 and 2024 (B); these are depicted by the yellow (first year) and red lines (second year), respectively.



The repeated patterns of detections on Motus stations suggests a common migratory path is taken by the majority of sparrows from this western region, both within and across populations. This suggests most birds in northern British Columbia, regardless of which side of the Rocky Mountains they breed on, migrate following the southern edge of the boreal forest across the Canadian prairies, and subsequently move southward along the western edge of the Eastern Temperate Forests in the United States. White-throated Sparrows travelling along this pathway are in line to pass by the Delta Marsh Bird Observatory in Manitoba where Mazerolle et al. (2005) found isotopic evidence that migrating sparrows captured at this location originated from British Columbia to northwestern Ontario. This suggests that birds from populations both west and east of the Rocky Mountains converge in the region of Manitoba (at the eastern edge of the Canadian Prairies, and west of the Great Lakes region on the Canada/U.S. border) before moving southward into the United States to wintering grounds. Unlike waterfowl that have "belt" like migratory routes (Buhnerkempe et al. 2016), our results suggest that the migratory connectivity of western White-throated Sparrows is more similar to that of Tree Swallows (*Tachycineta bicolor*), whereby individuals from different breeding populations increasingly converge along their way to the wintering grounds (Knight et al. 2018). However, unlike Tree Swallows, the majority of White-throated Sparrows in northern and central British Columbia converged on one region (south-central United States), instead of mixing on multiple wintering grounds (Knight et al. 2018).

Convergence of these western and central sparrow populations on a south-central U.S. wintering ground may account for the rapid spread of the doublet-ending songs across western and central Canada between 2000 and 2019 (Otter et al. 2020), which replaced the traditional triplet-ending songs as the dominant song variant during this period. Further evidence for winter tutoring was supported by later studies (Chartier 2021, Chartier et al. 2022) with the emergence, spread, and rapid rise in prevalence of the modulated-doublet ending song across western Canada between 2014 and 2020. Through the spatiotemporal overlap of birds with tutors from different populations during the winter, any learning biases in the acquisition of song types might promote this cultural exchange and spread of song variants. The current study, though, suggests this cultural transmission could be reinforced along return migration pathways. The migration routes used by our tracked birds overlaps the general breeding range of White-throated Sparrows across much of western Canada. Birds on return migrations to far western populations would sequentially encounter settled males or other migrating males from other breeding populations along their journey. If song acquisition is reinforced by tutors encountered during the birds' first breeding season (Nordby et al. 2001, Nulty et al. 2010, Mennill et al. 2018, Chartier et al. 2022), then the previously witnessed spread of song variants among White-throated Sparrow populations may be reinforced by both tutoring on common wintering grounds and along migratory pathways shared among breeding populations.

The result of the current analysis may also shed light on why, despite prominent cultural shifts in song across western and central Canada over the past two decades (Otter et al. 2020, Chartier 2021), these doublet-ending songs have not spread extensively into birds breeding in the Atlantic provinces of eastern Canada. Past banding studies suggest that birds breeding in these eastern populations migrate and winter in areas of the Atlantic region east of the Appalachian Mountains (Mazerolle et al. 2005); this would suggest less potential overlap on wintering grounds for which song variants can spread between western and eastern

breeding populations. Our study confirms that White-throated Sparrows Motus-tagged on a single eastern wintering ground (Georgia) largely migrated to breeding grounds northwest and northeast of the Appalachian Mountains, which would correspond to known breeding locations in eastern Ontario, southwestern Quebec, and eastward. This overlapped the general locations of the triplet-ending song variants posted to sound libraries over the past few years (Fig. 2). Past studies have confirmed the triplet-ending song variants are more pervasive on the wintering areas of the Atlantic coast east of the Appalachian Mountains (Otter et al. 2020, Chartier 2021), suggesting these variants may be reinforced on both wintering and migratory routes in these eastern populations.

Future directions

More extensive studies from a greater number of tagged breeding and wintering populations would shed additional light on the spatiotemporal isolation of different White-throated Sparrow populations and how this affects the spread of song variants. This could include investigation of migratory routes of birds tagged on breeding areas where the doublet-ending/triplet-ending song variants border (currently eastern Ontario/western Quebec in Canada) to determine whether the continued dialectal boundaries in this region are maintained by bifurcated migration paths that isolate birds onto different wintering grounds. Further, increasing the number of birds tagged on wintering grounds might reveal how birds overwintering in a shared location disperse among northern breeding areas. Elucidating which breeding populations converge on the isolated, western wintering grounds on the Pacific coast might also help understand how migratory connectivity of populations facilitates or impedes cultural evolution and song exchange in White-throated Sparrows.

Author Contributions:

Joel Khoo contributed to data collection, analysis, writing, and experimental design; Amie MacDonald contributed to funding acquisition, data collection, analysis, and editing; Inge-Jean Hansen contributed to funding acquisition, data collection, and editing; Cody Cox contributed to data collection and editing; Scott Ramsay contributed to funding acquisition, experimental design, data collection, and editing; Ken Otter contributed to experimental design, funding acquisition, data collection, analysis, writing, and editing.

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Data Availability:

Spatial data on White-throated Sparrow movements is available upon request from the Motus Wildlife Tracking Project (https://motus.org/) under White-throated Sparrow migration (#497). The list of recordings accessed and analyzed from the Macaulay Library of Sound are included as Appendix 1, including the file numbers that can be accessed online.

LITERATURE CITED

Baptista, L. F., and L. Petrinovich. 1984. Social interaction, sensitive phases and the song template hypothesis in the White-crowned Sparrow. Animal Behaviour 32:172-181. https://doi.org/10.1016/S0003-3472(84)80335-8

Birds Canada. 2024. Motus: fetch and use data from the Motus Wildlife Tracking System. Birds Canada, Port Rowan, Ontario, Canada. https://motusWTS.github.io/motus

Borror, D. J., and W. W. H. Gunn. 1965. Variation in White-throated Sparrow songs. Auk 82:26-47. https://doi.org/10.2307/4082793

Brenowitz, E. A., and M. D. Beecher. 2005. Song learning in birds: diversity and plasticity, opportunities and challenges. Trends in Neurosciences 28:127-132. https://doi.org/10.1016/j.tins.2005.01.004

Buhnerkempe, M. G., C. T. Webb, A. A. Merton, J. E. Buhnerkempe, G. H. Givens, R. S. Miller, and J. A. Hoeting. 2016. Identification of migratory bird flyways in North America using community detection on biological networks. Ecological Applications 26:740-751. https://doi.org/10.1890/15-0934

Byers, B. E., K. L. Belinsky, and R. A. Bentley. 2010. Independent cultural evolution of two song traditions in the Chestnut-sided Warbler. American Naturalist 176:476-489. https://doi.org/10.1086/656268

Chartier, S. L. 2021. Re-inventing an old hit: song evolution within and between populations of White-throated Sparrows. Thesis. University of Northern British Columbia, Prince George, British Columbia, Canada. https://www2.unbc.ca/sites/default/files/sections/ken-otter/schartiermscthesis-final.pdf

Chartier, S. L., S. M. Ramsay, and K. A. Otter. 2022. Within-population song evolution in White-throated Sparrows (*Zonotrichia albicollis*). Behaviour 159:1421-1445. https://doi.org/10.1163/1568539X-bja10184

DeWolfe, B. B., and L. F. Baptista. 1995. Singing behavior, song types on their wintering grounds and the question of leap-frog migration in Puget Sound White-crowned Sparrows. Condor 97:376-389. https://doi.org/10.2307/1369024

Falls, J. B., and J. G. Kopachena. 2020. White-throated Sparrow (*Zonotrichia albicollis*), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.whtspa.01

Garland, E. C., A. W. Goldizen, M. S Lilley, M. L. Rekdahl, C. Garrigue, R. Constantine, N. Daeschler Hauser, M. M. Poole, J. Robbins, and M. J. Noad. 2015. Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. Conservation Biology 29:1198-1207. https://doi.org/10.1111/cobi.12492

Garland, E. C. and P. K. McGregor. 2020. Cultural transmission, evolution, and revolution in vocal displays: insights from bird and whale song. Frontiers in Psychology 11:544929. https://doi.org/10.3389/fpsyg.2020.544929

Garland, E. C., L. Rendell, L. Lamoni, M. M. Poole, and M. J. Noad. 2017. Song hybridization events during revolutionary song change provide insights into cultural transmission in humpback whales. Proceedings of the National Academy of Sciences 114:7822-7829. https://doi.org/10.1073/pnas.1621072114

Garnier, S., N. Ross, R. Rudis, A. P. Camargo, M. Sciaini, and C. Scherer. 2023. viridis: colorblind-friendly color maps for R. https://github.com/sjmgarnier/viridis/ https://doi.org/10.32614/CRAN.package.viridis

Grolemund, G., and H. Wickham. 2011. Dates and times made easy with lubridate. Journal of Statistical Software 40:1-25. https://doi.org/10.18637/jss.v040.i03

Kahle, D., and H. Wickham. 2013. ggmap: spatial visualization with ggplot2. R Journal 5:144-161. https://doi.org/10.32614/RJ-2013-014

Knight, S. M., D. W. Bradley, R. G. Clark, E. A. Gow, M. Bélisle, L. L. Berzins, T. Blake, E. S. Bridge, L. Burke, R. D. Dawson, P. O. Dunn, D. Garant, G. L. Holroyd, D. J. T. Hussell, O. Lansdorp, A. J. Laughlin, M. L. Leonard, F. Pelletier, D. Shutler, L. Siefferman, C. M. Taylor, H. E. Trefry, C. M. Vleck, D. Vleck, D. W. Winkler, L. A. Whittingham, and D. R. Norris. 2018. Constructing and evaluating a continent-wide migratory songbird network across the annual cycle. Ecological Monographs 88:445-460. https://doi.org/10.1002/ecm.1298

Lachlan, R. F., O. Ratmann, and S. Nowicki. 2018. Cultural conformity generates extremely stable traditions in bird song. Nature Communications 9:2417. https://doi.org/10.1038/s41467-018-04728-1

Lemon, R. E., and M. Harris. 1974. The question of dialects in the songs of White-throated Sparrows. Canadian Journal of Zoology 52:83-98. https://doi.org/10.1139/z74-013

Marler, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. Journal of Comparative and Physiological Psychology 71:1-25. https://doi.org/10.1037/h0029144

Massicotte, P., and A. South. 2023. rnaturalearth: world map data from natural earth. https://doi.org/10.32614/CRAN.package.rnaturalearth

Mazerolle, D. F., K. A. Hobson, and L. I. Wassenaar. 2005. Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of White-throated Sparrows at a migration monitoring station. Oecologia 144:541-549. https://doi.org/10.1007/s00442-005-0031-6

Meidinger, D., and J. Pojar. 1991. Ecosystems of British Columbia. British Columbia Ministry of Forests Special Report Series 6, Victoria, British Columbia, Canada.

Mennill, D. J., S. M. Doucet, A. E. M. Newman, H. Williams, I. G. Moran, I. P. Thomas, B. K. Woodworth, and D. R. Norris. 2018. Wild birds learn song from experimental vocal tutors. Current Biology 28:3273-3278. https://doi.org/10.1016/j.cub.2018.08.011

Nelson, D. A. 2000. Song overproduction, selective attrition and song dialects in the White-crowned Sparrow. Animal Behaviour 60:887-898. https://doi.org/10.1006/anbe.2000.1560

Nordby, J. C., S. E. Campbell, and M. D. Beecher. 2001. Late song learning in song sparrows. Animal Behaviour 61:835-846. https://doi.org/10.1006/anbe.2000.1673

Nordby, J. C., S. E. Campbell, and M. D. Beecher. 2002. Adult song sparrows do not alter their song repertoires. Ethology 108:39-50. https://doi.org/10.1046/j.1439-0310.2002.00752.x

Nulty, B., J. M. Burt, Ç. Akçay, C. N. Templeton, S. E. Campbell, and M. D. Beecher. 2010. Song learning in Song Sparrows: relative importance of autumn vs. spring tutoring. Ethology 116:653-661. https://doi.org/10.1111/j.1439-0310.2010.01782.x

Otter, K. A., A. Mckenna, S. E. LaZerte, and S. M. Ramsay. 2020. Continent-wide shifts in song dialects of White-throated Sparrows. Current Biology 30:3231-3235. https://doi.org/10.1016/j.cub.2020.05.084

Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data. R Journal 10:439-446. https://doi.org/10.32614/RJ-2018-009

Petrinovich, L., and L. F. Baptista. 1987. Song development in the White-crowned Sparrow: modification of learned song. Animal Behaviour 35:961-974. https://doi.org/10.1016/S0003-3472(87)80153-7

Posit Team. 2023. RStudio: Integrated development environment for R. Posit Software, Boston, Massachusetts, USA. https://posit.co/products/open-source/rstudio/

QGIS Development Team. 2022. QGIS geographic information system. QGIS Association. http://www.qgis.org

R Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramsay, S. M., and K. A. Otter. 2015. Geographic variation in White-throated Sparrow song may arise through cultural drift. Journal of Ornithology 156:763-773. https://doi.org/10.1007/s10336-015-1183-8

Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335-337. https://www.jstor.org/stable/20065798

Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. Holberton, P. H. Loring, G. W. Mitchell, D. Norris, J. Paquet, R. A. Ronconi, J. Smetzer, P. A. Smith, L. J. Welch, and B. K. Woodworth. 2017. The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12(1):8. https://doi.org/10.5751/ACE-00953-120108

United States Environmental Protection Agency. 2023. Ecoregions of North America: level 1 ecoregions. Environmental Protection Agency, Washington, D.C., USA. https://www.epa.gov/eco-research/ecoregions-north-america

Wickham, H., M. Averick, J. Bryan, W. Chang, L. D. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, et al. 2019. Welcome to the tidyverse. Journal of Open Source Software 4:1686. https://doi.org/10.21105/joss.01686

Wickham, H., and K. Müller. 2022. DBI: R database interface. https://doi.org/10.32614/CRAN.package.DBI

Williams, H. and R. F. Lachlan. 2021. Evidence for cumulative cultural evolution in bird song. Philosophical Transactions of the Royal Society B 377:20200322. https://doi.org/10.1098/rstb.2020.0322

Zimmerman, H. D., S. M. Ramsay, V. Mesias, M. Mora, B. W. Murray, and K. A. Otter. 2016. Evolution of White-throated Sparrow song: regional variation through shift in terminal strophe type and length. Behaviour 153:1839-1861. https://doi.org/10.1163/1568539X-00003394

Appendix 1. White-throated Sparrow song classification.

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