

GEOGRAPHIC EVOLUTION OF THE WHITE THROATED SPARROW DIALECT

BY

ALEXANDRA MCKENNA

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Abstract

The Social Adaptation hypothesis of dialect formation in birds suggests that new song variants may become prominent in locations if they convey an advantage to signalling to neighbours. White-throated sparrows have two distinct dialects, songs ending in repeating doublets of notes (doublet-ending) or in repeating triplets (triplet-ending). Historically the triplet-ending dialect dominated North America, with only rare occurrences of doublet-ending dialects throughout Borror and Gunn's (1965) surveys across Canada. Following analysis of song records in BC and Alberta there appears to have been a noticeable eastward spread in the doublet-ending dialect. The start point of this spread appears to originate in a white-throated sparrow population in north-central British Columbia. White-throated sparrows appear to have invaded this region, secluded by the Rocky Mountains, in the 1940s, but early recordings in the 1950s confirmed the triplet-ending song to have been common amongst early breeders. By 2000, though, the doublet-ending dialect had become fixed in this western population. I analysed over 1000 recordings collected between 2000 and 2016 from across North America and found support for the spread of the dialect eastwards. The transition line between the doublet and triplet-ending dialects had been identified in 2004 to occur in eastern Alberta ($\sim 110^{\circ}00'$ W – Ramsay & Otter 2015). However, during the period of 2000-2009, regions that previously had birds singing triplet-ending songs have become dominated by doublet-ending dialects, starting with the Prairie Region (Alberta, Saskatchewan and Manitoba). By 2016, all recordings west of central Ontario ($\sim 79^{\circ}30'$ W) were doublet-ending songs, representing a spread of approximately 2200km over a 12-year period – 183km/year. A shift in bird song this rapid is unprecedented, this could support an evolutionary advantage to the doublet-ending dialect as predicted by the social adaptation hypothesis. Recordings over the next few years in key locations in eastern Ontario, Quebec, Northeastern United States and the Maritimes will be crucial to track the rate of continued spread. Research should also be conducted on what attributes the doublet-ending song has that is facilitating the spread, whether it is female preference or another advantage for the male's song.

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Table of Contents

Abstract	i
Acknowledgements	ii
List of Tables	iv
List of Figures	v
Introduction.....	1
Methods.....	6
Data Analysis	7
Kernel Density Estimation.....	8
Results.....	9
Discussion.....	11
Conclusion	13
References.....	20

List of Tables

Table 1. Descriptions of bird song sources containing their province/state region, number of recordings acquired and their approximate date ranges.....	15
Table 2. Number of doublet and triplet-ending songs from individual male white-throated sparrows recorded from 1951-2016 across four regions of North America.	16

List of Figures

Figure 1. Doublet-ending and triplet-ending songs from male white-throated sparrows in Algonquin Park, Ontario (Zimmerman et al 2016).....	17
Figure 2. Kernel Density Estimates of doublet and triplet-ending song recordings partitioned into three time categories of before 2000, from 2000-2009, and after 2009 (2010-2016). Doublet-ending song densities can be seen in the left figures in red, and triplet-ending song densities are shown in blue on the right. The number of recordings (n) is shown in the upper corner of each map. Bandwidth = 1, Grid size = (2000, 2000).	18
Figure 3. Comparison of Kernel Density Estimation of doublet and triplet-ending song recordings from Ontario in the years 2010-2016. Doublet-ending recordings are shown on the left in red and triplet-ending songs are shown in blue on the right. Bandwidth = 0.5, Grid size = (1000,1000).....	19

Introduction

Passerine birds, particularly males, use song to both advertise territorial tenure, and to attract mates (Catchpole & Slater 1995). Songs are learnt from audio tutors early in a bird's life (reviewed by Marler 1997), which can result in the emergence of song dialects - regionally-specific variations in song structure that is shared amongst neighbouring males. During the learning phase of song development, young males memorize songs they hear from adult tutors to whom they are exposed; simply by proximity these songs often reflect the variants present in the natal origin of the young males, especially if the birds do not migrate south until later in the year (Reif et al. 2015). This can reinforce certain song variants being more prolific in particular geographic regions (Podos & Warren 2007). Novelty, though, can initially arise during the production process, if males produce small copying errors in the songs they have learned. This results in a deviation from the original tutored song (Podos & Warren 2007), which if copied by subsequent generations can result in the emergence of new local song variants.

Populations of song birds often have a specific local dialect that has slight variations from dialects of other populations, designated as 'foreign dialects' (Kroodsma et al. 1976). These foreign dialects are often discriminated against by males within a specific population, more so than the local dialects. Male song birds tend to respond more to local dialects compared to foreign dialects, perceiving them as a greater threat to their territories and mates (Milligan & Verner 1971; Baker 1982; Wright & Dorin 2001). One means by which these results can be explained is through local song variants reflecting the genetic origin of an individual, and thus its likelihood of carrying locally-adapted traits – the local adaptation hypothesis (Payne 1981).

Local dialects can form if the sensitive phase of learning occurs post-fledging but prior to southern migration, predisposing the young males to learn the regional song type from local tutors (Payne 1981). If those young birds return to breed in their natal region, the result is strong congruence between the site of origin of the bird and the song variant it sings. If there is also selective pressure for locally-acquired adaptations that enhance other aspects of life histories – ability to gain local resource types or successfully breed in the local environment – these regional dialects could suffice to identify males as ‘locals’ and thus be favoured in mate choice (the local adaptation hypothesis of dialect formation -Payne 1981). A main assumption of this hypothesis is that juvenile birds must also return to their natal area to breed (Payne 1981). If females imprint on this local variant and prefer males who sing these dialects, sexual selection may lead to a decrease in gene flow among populations (Payne 1981).

An alternate theory of how regionalized song variants may arise has become known as the social adaptation hypothesis (Baker & Mewaldt 1978; Cunningham & Baker 1987; Marler 1997; Nelson 1999; Baker et al. 2006). Some birds are known to settle in non-natal regions, yet dialects still persist; this would suggest males in some species might adopt the locally-occurring songs from the males in the region in which they settle (Thompson 1970; Baker & Mewaldt 1978; Cunningham & Baker 1987; Marler 1997; Baker et al. 2006). Local dialects in these situations could take route if it is advantageous during song contests to sing something similar to your neighbour for such purposes as song-matching (the social adaptation hypothesis of dialect formation). Females can still use songs as a form of assortative mating strategy if there is an advantage of pairing to males singing a local song type (either as these males are better at defending territories – social adaptation hypothesis - or because this infers they may possess

locally-adapted traits – local adaptation hypothesis) (Baker et al. 2006). Females of some species preferentially mate with males who sing their natal dialect (MacDougall-Shakleton & Macdougall-Shakleton 2001), and in such instances, males singing a foreign song in a region would likely experience reduced pairing success, which can reinforce the formation of regional dialects (Baker & Mewaldt 1978; Baker et al. 2006).

In the social adaptation hypothesis, males learn songs in the regions to which they settle, rather than simply imprinting on the songs of their natal region. This requires explanations of how those songs arise. The selective attrition hypothesis predicts young birds will learn and memorize many songs during a sensitive period of learning, possibly copying songs of males from multiple breeding populations which are encountered on overlapping wintering ranges. Overproduction of song will occur in the following year as first-time breeders and the males will eventually discard the dialects that do match their neighbours (Nelson 1999; Marler 1997; Thompson 1970). The overproduction period gives the young males the flexibility to test out various song variants until they find one that accommodates local song dialects. Birds that are able to pare down their repertoire to those song variants that match their neighbours can communicate more effectively to surrounding birds (Nelson 1999). Counter to the selective attrition hypothesis, the late acquisition hypothesis predicts young birds delay final song production until post-settlement on first breeding territories, and converge on the song structure of neighbours whom they settle next to rather than learning many songs and selectively discarding those that do not match neighbors (Thompson 1970; Cunningham et al. 1987). By crystalizing their song after settlement, they can converge on the local variant and this makes interacting with neighbours more efficient (and potentially means they attract females who prefer

a local dialect) (Thompson 1970; Cunningham et al. 1987). This hypothesis assumes that the song crystallization phase is delayed until the male has settled into their breeding territory (Thompson 1970; Cunningham et al. 1987).

Both the social adaptation hypothesis and local adaptation hypothesis assume that regional song variation evolves as it conveys an advantage to the signaler. However, song variation may arise through non-adaptive mechanisms, include copying errors when young birds memorize and attempt to produce tutored songs (Podos & Warren 2007; Ramsay & Otter 2015). These small copying errors may in turn be copied by others, introducing a new song variant. It has been suggested that the likelihood of such errors taking root is greater in small, isolated populations where there are fewer tutors from whom to copy (Baker et al. 2006; Gammon 2007). Thus dialects may become introduced into novel geographic areas, such as on the edge of a species' distribution, and may be copied by others, particularly if there are a few alternate tutors.

Although variants might arise by chance copy errors, if the new song type conveys any adaptive advantage, the new dialect may spread among the population in a non-random fashion (Ramsay & Otter 2015, Zimmerman et al 2016). Adaptive functions could arise if they help facilitate social communication (social adaptation hypothesis above) or increase transmission of the signal in the new environment, such as propagating better through urban noise (LaZerte et al. 2015). Thus, regional dialects may arise through a variety of adaptive or non-adaptive mechanisms, but if new song variants convey some advantage they could begin to spread quickly through populations.

I studied such a shift in song dialect in the white-throated sparrow (*Zonotricha albicollis*). The main breeding range of the white-throated sparrow is the boreal forests across Canada. Most of the species range occurs east of the Rocky Mountains, ranging from the eastern Yukon through Newfoundland in Canada; however, there is a breeding population west of the Rocky Mountains in the central interior of northern British Columbia. This breeding population appears to have become established in the mid 1940's (Munro 1949), with a new wintering range in California emerging shortly thereafter. This breeding and wintering population has largely increased since its establishment and might be partially isolated from the eastern breeding and wintering location. The discontinuity between this eastern and western population may have resulted in the formation of a distinct song variant among the western white-throated sparrows (Ramsay & Otter 2015). The western population sings a doublet-ending song, meaning there is a repeating unit of two notes in the terminal phrase (or strophe), while the eastern population exhibits the more species-typical triplet-ending song where the terminal strophes has a repeating unit of three notes (Ramsay & Otter 2015).

Prior to the formation of this new western colony, the triplet-ending dialect was the most prominent song variant across all breeding regions, with the primary variation in song among males being in the starting phrase before the terminal repeating units (Borror & Gunn 1965; Lemon and Harris 1973); this starting phrase, which includes three to four ascending or descending whistled notes, is sufficiently variable among males within populations to facilitate neighbour-to-neighbour recognition and discrimination (Lemon & Harris 1973). Borror & Gunn's (1965) initial surveys of white-throated sparrow songs included males in central British Columbia, and all these original recordings from the 1950s were males singing triplet-ending

songs characteristic of the rest of Canada at that time (Zimmerman et al. 2016). However, sometime between these early recordings and the turn of the century (2000), the doublet-ending songs had spread to fixation among male white-throated sparrows west of the Rocky's and appears to be spreading eastwards into Alberta (Zimmerman et al. 2016).

To determine the extent of dialectal variation on a continental scale, and assess whether there is direct evidence of this eastward spread, I analyzed song recordings from various sources - including personal recordings and birding websites - collected from 2000 through 2016 across North America. I used these recordings to determine the locations of current and past boundary lines for the dialect shift and to determine the rate at which the dialect is spreading. I also analyzed historic songs from 1950 onward, to determine approximately when and where the doublet-ending dialect became present in western populations. Present day recordings were analyzed to determine the rate of shift of the dialect as well as the proportion of doublet-ending to triplet-ending songs among present populations. An increase in prevalence of doublet-ending songs in eastern populations (where triplet-ending songs have continued to predominate over the past 50 years since Borror & Gunn's original surveys) might suggest some advantage of doublet-ending song in social signaling.

Methods

I analyzed audio recordings from 1951-2016 from white-throated sparrow populations across North America from various sources, including: personal recordings made by myself, collaborating researchers in the project or researchers donating recordings made as a result of other sound studies; contributed recordings made by citizen scientists and uploaded to sound

libraries; and finally from recorded Breeding Bird Surveys (BBS) conducted by biologists of the federal government (see Table 1). Overall, 1256 songs were collected from all the above sources and pooled in a data set and analyzed to examine the evolution in the terminal strophe over time.

Data Analysis

I analyzed song recordings using spectrograms in Audacity 2.0.6, Avisoft SASLab Pro 5.2.07, Avichorus, and Xeno-canto. Song were recorded from the majority of the provinces in Canada as well as US States (Table 2). The audio recordings of males were classified as either doublet or triplet-ending strophes (See Ramsay & Otter 2015 for description of classification). Doublet-ending songs have a distinct two note repeat system following the introductory phrase, while triplet-ending songs follow the intro phrase with a 3 note repeat system (Figure 1). These differences are easily detectable on spectrographic software, like Audacity, or websites with embedded spectrograms (Avichorus and Xeno-Canto), but once trained can also be detected by ear. The location coordinates (latitude/longitude) were noted for each recording, if the exact location was unknown the latitude and longitude of the named recording location was used. I split the geographic regions into time periods of 1951-1999, 2000-2009, 2010-2016 to investigate the evolution of the dialect shift from historic recordings to present day across North America. These time units allowed for sufficient numbers of recordings for the large geographic regions being covered.

For the song to be appropriately classified, the recording had to include two or more repeating phrases in the terminal strophe so that the ending type could be unambiguously categorized. All

data from all sources were pooled and compared for the density of doublet and triplet-ending songs as the years progressed. Proportions of doublet and triplet-ending songs were also calculated in four regions across North America: the Western region (BC, California and Washington); the Prairies region (Alberta, Saskatchewan, Manitoba, and Northwest Territories); Ontario/central (Ontario, Illinois, New York, Michigan, Minnesota, and Wisconsin); and Quebec and the Maritimes region (Delaware, Georgia, Maryland, Newfoundland, Nova Scotia, Maine, New Hampshire, Massachusetts, Pennsylvania, Quebec, and Vermont). The total number of males in each region singing either doublet or triplet-ending songs were then categorized by time periods when recordings were made - 1951-1999, 2000-2009, and 2010-2016 - to examine the changes in proportion of males singing each song variant from historic recordings to present day recordings. These proportions were then analyzed with a Fisher Exact test.

Kernel Density Estimation

I used the package `KernSmooth2.23` (Wand & Jones 1995) in R (vs 3.3.2 R Development Core) to create kernel density estimates associated with the locations of males singing either doublet or triplet-ending songs. Kernel Density Estimates (KDE) determine the density of observations associated with specific geographic locations, utilizing grids overlain on the region and estimating the number of observations within a bandwidth radius from the center of each cell. These are used to create density polygons representing high to low occurrence of observations. For example, KDE analysis has been used in various investigations to determine the difference between victim and criminal fiber strands in crime scenes (Evetts et al. 1987), as well as identify locations of high-crime neighbourhoods from crime statistics for coordinating policing efforts (Hart & Zandbergen 2014; Chainey 2013). For the full analysis of songs across North America, I

used a bandwidth of 1 and grid size of 2000x2000 and grouped males based on which song variant they sang and from which years the recordings were collected. Recordings were partitioned into those made prior to 2000, between 2000-2009 and from 2010-2016. For the focal study of song variants in Ontario from 2010 onwards, I used a smaller bandwidth of 0.5 and grid size of 1000x1000. Bandwidth and grid size decisions were based on which combinations gave the best clarity to spatial distinctions.

Results

Songs in the Western, Prairies and Ontario/Central regions revealed a shift over time in the numbers of males singing doublet-ending songs compared to triplet-ending songs. The western region likely shifted in dialects first, with 8 triplet-ending dialects recorded out of 11 recordings before 2000 and zero out of 205 recorded from 2000-2016 (Fisher Exact Test $p < 0.0001$) (Table 2). The Prairies likely shifted next with 7 triplet-ending dialects recorded out of 7 recordings before 2000 and 22 out of 141 recordings after 2000 (Fisher Exact Test $p < 0.0001$) (Table 2). Ontario/Central appears to be the most recent to have a shift in dialect proportions with 57 out of 57 songs being triplet-ending songs before 2000 and 393 out of 629 recordings being triplet-ending songs after 2000 (Fisher Exact Test $p < 0.0001$) (Table 2). Quebec and the Maritimes had no significant shift in their dialect proportions, remaining with a dominant triplet-ending dialect, suggesting that the dialect boundary has not reached these regions. Song recordings in Quebec and the Maritimes showed no significant change with time, with 22 out of 22 being triplet-ending dialects historically (1951-2000) and 148 out of 150 being triplet-ending songs from 2000-2016 (Fisher Exact Test $p = 0.75$) (Table 2).

Prior to 2000, the triplet-ending dialect was dominant across Canada, with only 3 recorded doublet-ending dialects present in BC (Figure 2). There were no recorded doublet-ending dialects anywhere else across Canada in recordings from the 1950s/60s or sporadic recordings in the next three decades (1950-2000). However, by 2000 all birds recorded west of the Rockies, and several recorded north east of the Rockies were singing doublet-ending songs, suggesting the doublet-ending dialect emerged in western Canada. 2000-2009 is a transitioning period for the white-throated sparrow dialect. All 133 songs recorded in western Canada between 2000-2009 were doublet-ending, while in Ontario/Central 130 of 139 songs recorded during the same period were triplet-ending. During this period, song recordings from the Prairie's region appeared to be in transition, with 54 of 76 recorded songs being doublet-ending (Table 2). These same patterns are revealed in kernel density estimates which show a progressive eastward spread of the doublet-ending song variant (Figure 2).

Currently, the dialect boundary appears to be in Eastern Ontario (Figure 3). From songs recorded between 2010 through 2016, the doublet-ending song appears to have spread to ubiquity throughout western Ontario, with the majority of the triplet-ending songs being seen in eastern Ontario near Algonquin Park, where other white-throated sparrow studies have been focused (Ramsay & Otter 2015). Previous song records prior to 2000 had zero doublet-ending songs recorded in Ontario and only 9 doublet-ending songs out of 139 songs recorded from 2000-2009 (Table 2). The spread of this dialect is occurring at very fast rates, switching from predominately triplet-ending songs prior to 2000 in western Ontario and evolving to majority doublet-ending songs by 2010. In surveys conducted across Alberta in 2004, Ramsay and Otter (2015) found the transition from doublet-ending to triplet-ending songs had largely occurred by

the eastern edge of the province ($\sim 110^{\circ}00'$ W). Given that by 2016, all recordings west of central Ontario ($\sim 79^{\circ}30'$ W) are doublet-ending, this represents a spread of nearly 2200km over a 12 year period – 183km/year.

Discussion

Doublet and triplet-ending dialects have recently been shifting in prevalence geographically, the doublet-ending dialect has surpassed its previous western boundaries from the early 2000's and has now become a common song in eastern provinces like Ontario. The rate of spread of one song type at the expense of another song type that our data suggest is unprecedented. The doublet-ending dialect has completely usurped the triplet-ending dialect across western North America over the last ten years. Since the doublet-ending dialect has spread to ubiquity regionally and has not become intermixed randomly with triplet-ending singers in each population, this suggests there is an underlying advantage to the doublet-ending song variant. The doublet-ending may have initially arisen in central BC through random copying errors or drift, becoming more common because of a relatively smaller, more isolated population. This could potentially explain the dialect spreading to ubiquity regionally, but not the consistent transition eastward into the larger breeding populations. The eastward spread of this dialect at the expense of the triplet-ending songs suggests some advantage conveyed by the doublet-ending song in either inter-sexual or intra-sexual signaling, and thus support predictions of the social adaptation hypotheses of dialect formation. Such transitions would not be expected under the local adaptation hypothesis; that hypothesis assumes that the young males learn their songs from tutors on natal grounds in which the young also return to breed, and these song variants convey information on local genes (Payne 1981). Under such a scenario, novel song types from

neighbouring dialect regions would be selected against and not be predicted to spread at the expense of local dialects.

If doublet-ending songs do convey an advantage to males, the next question is how these might spread from one region to another. One possible explanation for the spread among breeding populations is if males intermix with foreign tutors on wintering grounds. In 2013 Otter & Ramsay (K.A. Otter & R.M. Ramsay, unpublished data) conducted a pilot geolocator study on twenty doublet-ending singing white-throated sparrows breeding in Prince George, BC. These geolocators have a photo sensor that sticks out from the birds' feathers and measures light every two minutes for up to two years. The following summer they recovered four geolocators from returning birds to identify wintering locations. Rather than north-central BC birds solely using California breeding grounds as had been previously suggested, three of the four returning males had overwintered in the eastern United States (East Texas region), while one had travelled south down the west coast and wintered in California. The three birds that wintered in the eastern United States shared a wintering ground known to be used by white-throated sparrows breeding across the northern Prairie regions in Canada. This could suggest that our doublet-ending singing males could be tutoring the natal triplet-singing males on these wintering grounds. This would facilitate the spread of the song, especially if it lends an advantage to those males that acquire it.

Historically, triplet-ending songs were most prominent among all populations of white-throated sparrows (Borror & Gunn 1965). Doublet-ending strophes were rarely present in populations in Borror and Gunn's initial surveys. The distribution of doublet-ending songs gradually began to

become more prominent across western geographic ranges just after 2000. After the doublet-ending dialect became the more prominent of the two songs in western populations including BC and Alberta it began to transition eastwards. This dialect boundary is likely still in motion eastwards, as more doublet-ending songs in these areas appear yearly. In just sixty years of song records the historically prominent triplet-ending dialect has gone from ubiquity to a solely eastern dialect, whereas the doublet-ending dialect has gone from a historically minority dialect to dominating western and central North American populations.

Future recordings should target the crucial transition and boundary areas like eastern Ontario, Quebec, Northeastern United States and the Maritimes to track and monitor the rate of continued spread. Further research should also be conducted on what attributes the doublet-ending song has that is facilitating the spread whether it is female preference or an underlying advantage in male-male signaling.

Conclusion

White-throated sparrow songs have shifted from dominantly triplet-ending to doublet-ending songs recently in western and central North America. Evidence from song records suggests this song variant arose from populations west of the Rockies, where the dialect then began to transition eastward, eventually reaching ubiquity up to central Ontario. The doublet-ending song now appears to be extending into eastern Ontario, with western and central Ontario dominantly doublet-ending singing populations. In contrast, Quebec and the Maritimes are still dominantly triplet-ending songs. Our song record data suggests potential evolutionary advantages of the doublet-ending dialect over the triplet-ending dialect, due to almost complete replacement of the

traditional song type across vast regions of western Canada. This known boundary line leaves a window of opportunity to observe the movement of this dialect as it is happening. Therefore, song recordings should be heavily focused in eastern North America to allow the transition line to be tracked annually. If the advantages of this doublet-ending dialect are strong enough there may be no presence of triplet-ending dialects in future generations. Therefore, future studies should focus their efforts on determining potential theories to explain any advantages that the doublet-ending dialect may hold.

Table 1. Descriptions of bird song sources containing their province/state region, number of recordings acquired and their approximate date ranges.

Source	Description	Geographic Locations	Date Range	Number of Recordings
Xeno-canto	Citizen scientist bird song data base	Canada: AB, BC, NL, NS, ON, QC, SK US: CA, CO, DE, GA, IL, ME, MI, MN, NH, NY, PA, TN, WA, WI	1999-2016	88
Avichorus	Breeding bird survey database using Autonomous Recording Units	Canada: NL, NT, ON, QC,	2004-2015	349
Macauley Library	Bird song data base	Canada: AB, BC, MB, ON, QB US: ME, MD, MA, MI, MN, NH, NY, VT	1950-2016	103
Jenn Foote	Donated personal recordings, using Autonomous Recording Units	Canada: ON	2011-2012	20
Dr. Ken Otter	Donated Personal recordings	Canada: AB, BC	1999-2014	225
Dr. Scott Ramsay	Donated Personal recordings	Canada: AB, ON	2004-2014	471

Table 2. Number of doublet and triplet-ending songs from individual male white-throated sparrows recorded from 1951-2016 across four regions of North America.

Year	Western		Prairies		Ontario/Central		Quebec/Maritimes	
	Doublet	Triplet	Doublet	Triplet	Doublet	Triplet	Doublet	Triplet
> 2000	3	8	0	7	0	57	0	22
2000-2009	133	0	54	22	9	130	0	3
2010-2016	72	0	87	0	227	263	2	145

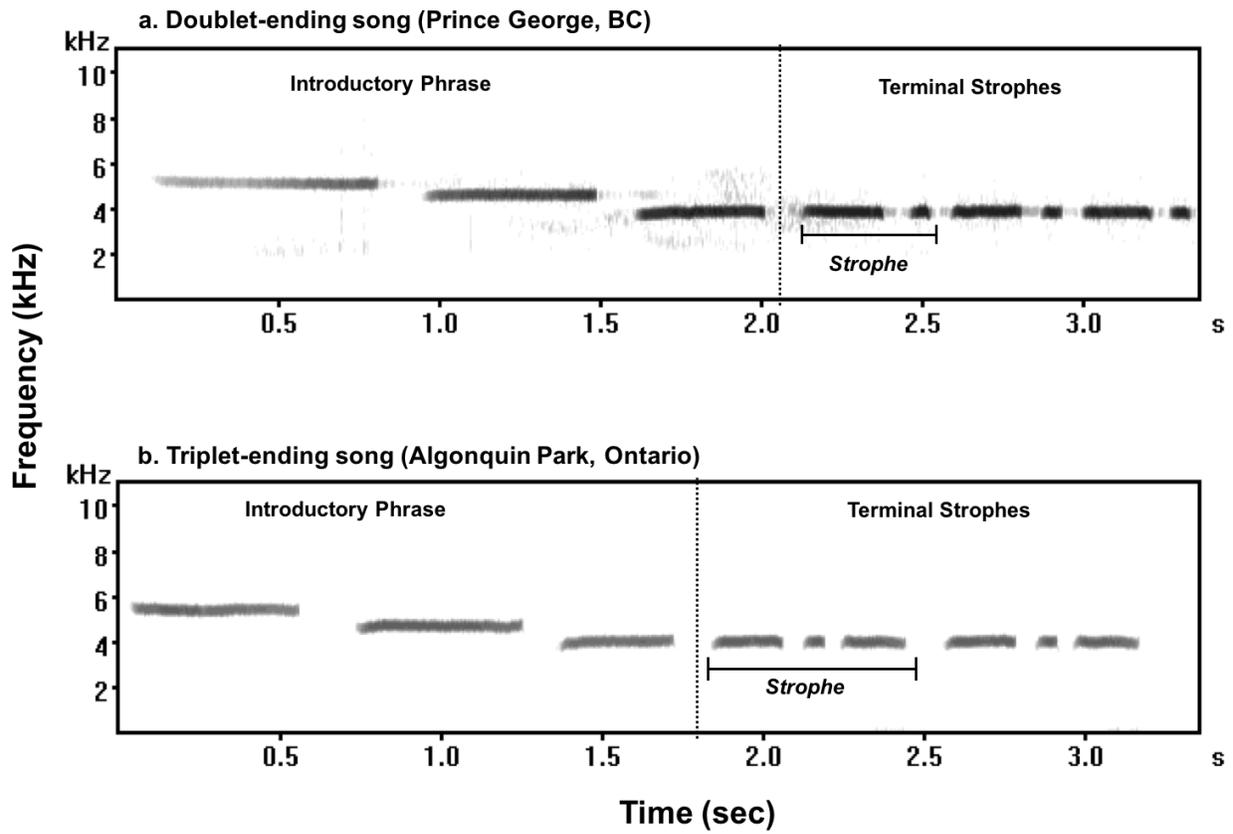


Figure 1. Doublet-ending and triplet-ending songs from male white-throated sparrows in Algonquin Park, Ontario (Zimmerman et al 2016).

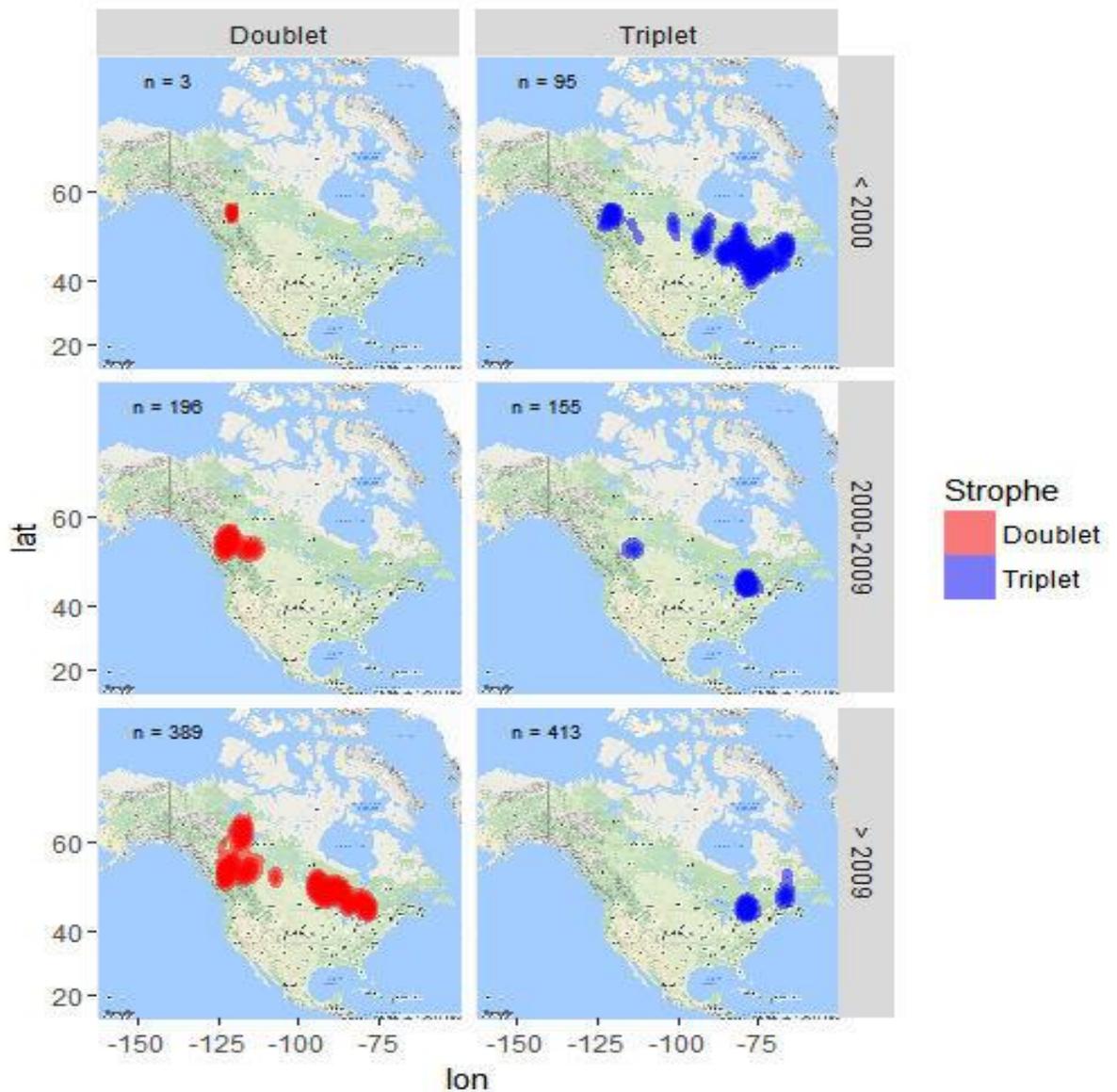


Figure 2. Kernel Density Estimates of doublet and triplet-ending song recordings partitioned into three time categories of before 2000, from 2000-2009, and after 2009 (2010-2016). Doublet-ending song densities can be seen in the left figures in red, and triplet-ending song densities are shown in blue on the right. The number of recordings (n) is shown in the upper corner of each map. Bandwidth = 1, Grid size = (2000, 2000).

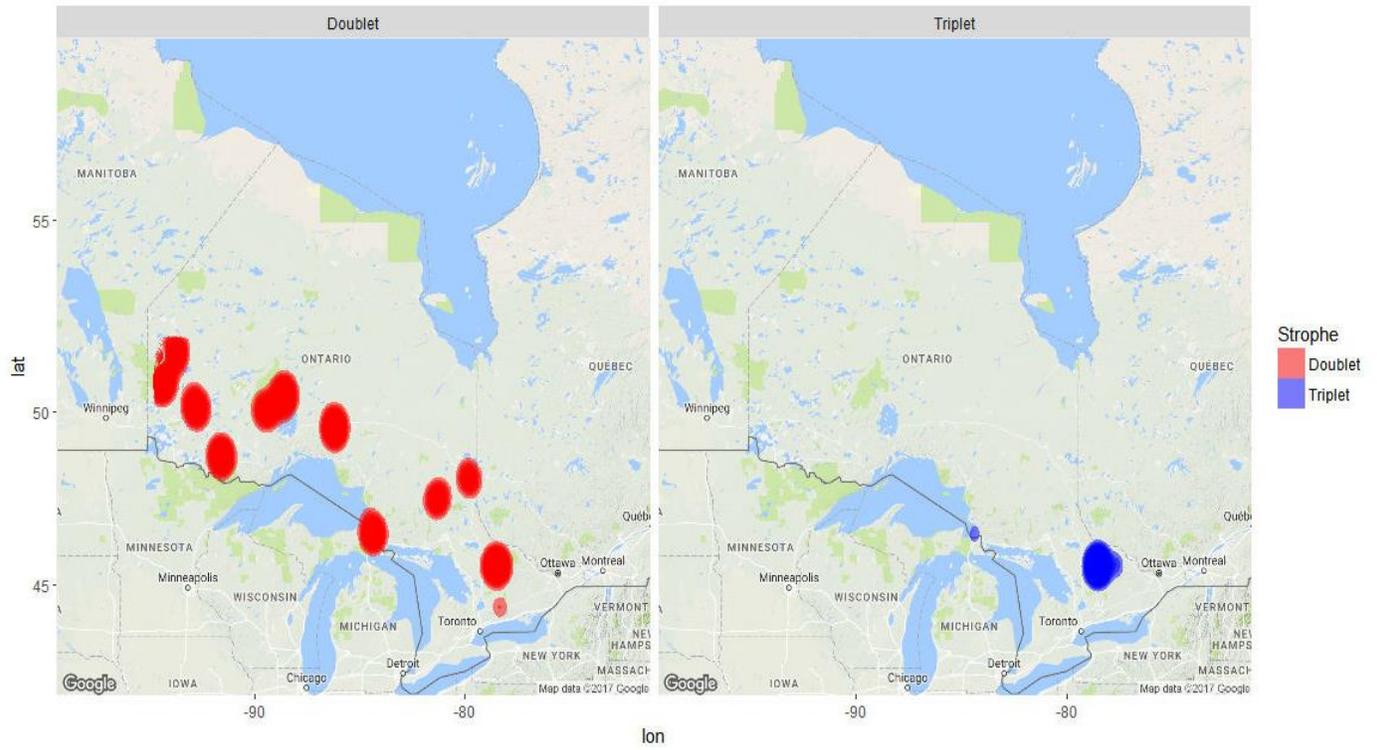


Figure 3. Comparison of Kernel Density Estimation of doublet and triplet-ending song recordings from Ontario in the years 2010-2016. Doublet-ending recordings are shown on the left in red and triplet-ending songs are shown in blue on the right. Bandwidth = 0.5, Grid size = (1000,1000).

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