AN ABSTRACT FOR THE THESIS OF

Anthony C. Dalisio for the Master of Science Degree

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Title: Song Dialects in Alpine-breeding Songbirds of the Rocky Mountains

Abstract approved:

Song dialects have been well documented among isolated bird populations. Natural fragmentation of bird populations among elevationally-restricted life zones could promote dialects in songbirds that use these habitats. I investigated dialect patterns among populations of songbird species breeding in isolated alpine life zones in the Rocky Mountains of Colorado. In 2010 and 2011, I recorded songs of Horned Larks (*Eremophila alpestris*), American Pipits (*Anthus rubescens alticola*), Wilson's Warblers (*Cardellina pusilla pileolata*), White-crowned Sparrows (*Zonotrichia leucophrys oriantha*), and Brown-capped Rosy-finches (*Leucosticte australis*) across 19 sites among six mountain ranges in Colorado. I digitally recorded songs and used spectrographic cross-correlation (SPCC) to calculate time-frequency similarity coefficients from pair-wise comparisons of song phrases among birds. Dialects were considered evident in a species if mean, within-site song similarity was greater than mean similarity among songs from across all sites. I also used Spearman-rank correlation to determine if song similarity among paired sites was related to distance between sites (range: 3 –189 km). I did not find Horned Larks and Brown-capped Rosy Finches in large enough sample sizes to document song-sharing patterns.

Within-site song similarity was greater than mean, across-site similarity for four of six populations in the American Pipit, two of four populations in the Wilson's Warbler and, four of five populations in the White-crowned Sparrow in 2010.

In 2011 I recorded birds at multiple sites within each of several contiguous alpine habitats in separate mountain ranges. This was done to test for decay in song similarity with distance within alpine habitat as well as among alpine isolates. In that year mean song similarity within site was greater than mean, across-site similarity for six of eight populations in the American Pipit, five of nine populations in the Wilson's Warbler and, eight of nine populations in the White-crowned Sparrow. In 2011 song similarity within ranges (among multiple sites) was greater than similarity across all birds in two of four mountain-range populations in the American Pipit, Wilson's Warbler, and the White-crowned Sparrow. Cluster analysis showed that White-crowned Sparrow songs were generally similar among sites in contiguous alpine habitat within mountain ranges, but there was no such clustering within American Pipit and Wilson's Warbler populations within mountain ranges. Song similarity in the American Pipit or the Wilson's Warbler was not related to between-site distance. Song similarity in the White-crowned Sparrow decreased with distance between sites, within contiguous alpine habitat in the data from 2011, but not between mountain ranges. My results provide evidence for the existence of dialects among American Pipit and White-crowned Sparrow populations in Colorado, though dialects in the latter species could be explained by clinal variation rather than by divergence among isolated alpine fragments.

Song Dialects in Alpine-breeding Songbirds
of the Rocky Mountains

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By
Anthony Carmen Dalisio
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Approved by Major Advisor
Dr. William E.Jensen

Approved by Committee Member
Dr. Dwight W. Moore

Approved by Committee Member
Dr. Marshall D. Sundberg

Approved by the Department Chair
Dr. R. Brent Thomas

Approved by the Dean of Graduate School
And Distance Education
Dr. Kathy Ermler

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PREFACE

My thesis contains a single chapter. It follows the format guidelines of the journal *The Condor*; to which I intend to submit this manuscript to for extramural publication. The Animal Care and Use Committee at Emporia State University approved all research procedures (ESU-ACUC-09-020).

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CHAPTER 1

INTRODUCTION

Vertebrate animals commonly use vocalizations to signal the identity and actions of individuals, genders, and species (Bradbury and Verhencamp 1998). Qualities of vocalizations within species can vary temporally and among geographical populations (Seppanen et al. 2007, Catchpole and Slater 2008). Such geographic patterns are commonly referred to as dialects (Kroodsma 2004). Dialects are widely exhibited among vertebrates (e.g., humans, Wolfram and Schilling-Estes 1998; frogs, Wycherley et al. 2002; whales, Deecke et al. 2000; and birds, Gill 2007).

Among the non-human vertebrates, the songs of birds are among the most familiar animal vocalizations. Birds (typically males in temperate latitudes) use song to signal their identity to potential mates and to competitors for those mates in defense of breeding territories (Beecher and Brenowitz 2005). Most young oscine songbirds learn their songs by imitating their fathers or neighbors during a formative phase of neurological development (Catchpole and Slater 2008). Thus, birds exhibit cultural traditions (Ryan 2006, Laland and Janik 2006, Laiolo and Tella 2007), where songs are passed generationally and among neighboring territory holders. An emergent result is spatial clustering of song similarity (i.e., dialects) which may be evident within and among bird populations (Payne 1981, Kroodsma 2004).

Dialects in songbirds have been of great interest in the past half-century of ornithology (Konishi 1965; Lemon 1975; Baker and Cunningham 1985;

Kroodsma 1996; Catchpole and Slater 2008). Researchers have commonly demonstrated spatial clustering of song similarity within—and song divergence among—populations of songbird species (e.g., White-crowned Sparrow, *Zonotrichia leucophrys*, Marler and Tamura 1962; Bobolink, *Dolichonyx oryzivorus*, Avery and Oring 1977; Indigo Bunting, *Passerina cyanea*, Payne 1982; Bewick’s Wren, *Thryomanes bewickii*, Kroodsma 1985; Blue Tit, *Cyanistes caeruleus*, Doutrelant et al. 1999; and Song Sparrow, *Melospiza melodia*, Foote and Barber 2007).

Geographic partitioning of songbird populations appears to promote song dialect formation. Such patterning is perhaps best exemplified among birds occupying discrete, oceanic islands (Newton 2003). Many species dispersed across oceanic islands and neighboring mainland exhibit patterns of song sharing within—and divergence among—their respective island populations (e.g., Fox Sparrow, *Passerella iliaca*, Naugler and Smith 1991; Chaffinch, *Fringilla coelebs*, Lynch and Baker 1994; Black-Capped Chickadee, *Poecile atricapillus*, Kroodsma et al. 1999; Sedge Wrens, *Cistothorus platensis*, Kroodsma et al. 2002). Song divergence among isolated bird populations may presage genetic divergence among such populations and eventual speciation (Slabberkoorn and Smith 2002).

Terrestrial islands of habitat exist within landscape matrices of less hospitable habitat (MacArthur and Wilson 1967). For example, distinct plant communities are stratified elevationally among “life zones” in montane ecosystems (Daubenmire 1938), creating “sky islands” of alpine habitats isolated by lower-elevation coniferous forests (Heald 1951, Carlquist 1965). In addition to characteristic flora, these sky-“islands” of habitat possess unique, isolated avifauna (Marshall 1957, Newton 2003). Examples of bird species occupying high-elevation life zones in the mountainous western United States include sub-populations of the White-Crowned Sparrow (*Zonotrichia leucophrys oriantha*; Chilton et al. 1995) and Brown-capped Rosy-finch (*Leucosticte australis*; Johnson et al. 2000). Among several alpine breeding birds in North America, only the White-Crowned Sparrow and the Lincoln’s Sparrow has been studied with regard to dialects among mountaintop populations (Baker 1975; Orejuela and Morton 1975; Baptista and King 1980; Baptista and Morton 1982; Harbison et al. 1999; Cicero and Brenowitz-Fredericks 2000, MacDougall-Shackleton and MacDougall-Shackleton 2001).

Given the evidence of song dialects among oceanic-island populations of birds, I expected that such dialects would be widely exhibited among sky-island populations of alpine-breeding bird species. My objectives for this study were to determine (1) if breeding songbird populations isolated among alpine sky islands exhibited divergence in shared song qualities (i.e., “dialects”) within species and (2) if any such divergence was a function of categorical isolation or an emergent property of microgeographic song variation where song similarity degrades clinally with distance between populations. The study species for my investigation included alpine-breeding populations of the Horned Lark (*Eremophila alpestris*), American Pipit (*Anthus rubescens alticola*), Wilson’s Warbler (*Cardellina pusilla pileolata*), White-Crowned Sparrow, and the Brown-capped Rosy-Finch. These five species were selected 1) due to their elevationally-isolated breeding populations among alpine habitats, 2) because they are geographically-stable during the breeding season rather than mobile cultural units, and 3) due to their relatively simple song repertoires that minimized ambiguity in the determination of dialects. Additionally, the song biology of all species but the White-crowned Sparrow has not been well investigated (Verbeek and Hendricks 1994; Beason 1995; Ammon and Gilbert 1999; Johnson et al. 2000).

METHODS

STUDY SPECIES

I attempted to record the songs of male Horned Larks, American Pipits, Wilson's Warblers, Mountain White-crowned Sparrows, and Brown-capped Rosy-finches on their alpine breeding territories for this study. However, I did not record large enough sample sizes of Horned Larks and Brown-capped Rosy Finches to report on song-sharing patterns for these species. The remaining target species were found breeding in relatively dense populations within the alpine sites I surveyed.

A single song type comprises the repertoires of the American Pipit, Wilson's Warbler, and White-crowned Sparrow (Verbeek and Hendricks 1994; Chilton et al. 1995; Ammon and Gilbert 1999). However, each species sings a different number of phrases (i.e., units within songs that are combinations of notes that regularly occur together; Petruskova et al. 2010) within their single song type. American Pipits sing one or two phrase types during song bouts, and Wilson's

Warblers (*C. p. pileolata*) sing one phrase type. White-crowned Sparrows typically sing three to five phrase types (Harbison et al. 1999). The American Pipit sings during flight, while the Wilson’s Warbler and White-crowned Sparrow do so while perched (Verbeek and Hendricks 1994; Chilton et al. 1995; Ammon and Gilbert 1999). Contrasts in singing behavior among these species have been attributed to the difference in nesting habitat: those species that sing while flying nest in the low-lying tundra vegetation, and those species that sing from perched positions nest in shrubs (Hendricks 1978).

STUDY AREA / POPULATIONS

I collected data among the naturally-fragmented alpine habitats of the Rocky Mountains of Colorado. Alpine habitat was fragmented by lower elevation coniferous forest, and was typically comprised of tundra grasses and forbs, low-lying shrubs, and granite outcroppings. I surveyed alpine habitats that occurred between 3500 and 4200 m in Rocky Mountain National Park (National Park Service), and in the Arapaho, Medicine Bow-Routt, Pike, and San Isabel National Forest lands (U.S. Forest Service).

I recorded songs on 10 sites (alpine habitat containing greater than five breeding individuals of a target species) across six mountain ranges in 2010: Front, Rabbit Ears, Rampart, Chicago, Ten Mile, and Sawatch (Table 1). Additionally, I recorded songs on 17 sites across four mountain ranges in 2011: Front, Chicago, Ten Mile, and Sawatch (Table1). In 2011, I located a subset of sites within contiguous, alpine habitat spaced 3 to 15.5 km apart. In both years I selected mountain ranges from 38 to 189 km apart. I recorded individuals of each target species at single locations per each mountain range in 2010.

Song divergence among isolated alpine habitats could be due to categorical isolation, where a geographical barrier restricts cultural transmission (Koetz et al. 2007), or simply isolation by distance, where song similarity merely decays with distance, as could happen within an otherwise contiguous population (Schook et al. 2008). Multiple (2-3), sites within a contiguous alpine patch per mountain range were used in 2011 to determine if song similarity was retained within such contiguous islands but diverged among disjunct alpine zones among mountain ranges.

SONG RECORDING

Song recording was performed daily during June and July in 2010 and 2011, after substantial snowmelt and the arrival of the study species. I recorded songs of target species in early June (14 to 26 June) and again during late June / early July (27 June to 12 July) in 2010 to quantify potential intra-annual variation in songs. Song sharing patterns remained stable through the breeding season of 2010 (see Results); thus, I recorded the songs of target species only once at each site in 2011(2 June to 5 July). Song recordings were made using a Marantz PMD-670 compact flash recorder and a Sennheiser MKH70 long shotgun microphone from a distance of no more than 50 m from target subjects. I recorded individual birds' songs multiple times within a single sampling session to maximize the number of songs with minimal background noise (Schook et al.

2008). A global positioning system (GPS) was used to record Universal Transverse Mercator coordinates of recorded birds. I downloaded and archived digital sound files of recorded bird songs onto a laptop CPU and external hard drives.

ANALYSES

I analyzed digital sound files graphically from sound spectrograms generated in RAVEN PRO, 1.4 (Cornell Lab of Ornithology, Ithaca, NY) that illustrate changes in song frequency (kHz) over time. Songs per species were categorized into song types and sub-categorized into phrase types (Fig. 1). I used spectrographic cross-correlation (SPCC) (Clark et al 1987; Cortopassi and Bradbury 2000; Baker and Logue 2003) to quantitatively evaluate similarity of song and phrase-types between all possible pair-wise combinations of recorded individuals per species. The correlation coefficients generated from SPCC were used to calculate mean song similarity within sites and mean song similarity across all birds, across sites, within a given species. Inference of song dialects was made if mean song similarity within sites was greater than mean song similarity across all birds, across sites. Because some sites in 2011 were within contiguous alpine habitat on a mountain range, mean similarity among birds, across sites within mountain ranges was calculated to determine if songs within these ranges were more similar to one another than mean similarity of song across all ranges.

I determined the relationship between song similarity and geographic distance in two ways. First, hierarchical UPGMA (Unweighted Pair Group

Method with Arithmetic mean) cluster-analysis (Euclidean distance) was used on data from 2011 when multiple sites were located within contiguous alpine habitat. This analysis yielded branching dendrograms illustrating divergence in song characteristics among the recorded populations. Cluster analysis output included cophenetic correlation coefficients (CPCC) that demonstrated how well dendrograms fit the similarity matrices from which they were derived (Sokal and Rohlf 1962). Second, I used Spearman-rank correlation to determine if mean song similarity between paired mountain ranges was related to distance (km) between mountain ranges ($\alpha = 0.05$). I also used Spearman-rank correlation coefficients (r_s) on 2011 data to determine if mean song similarity between paired sites within contiguous alpine habitat on mountain ranges was related to distance between sites within those ranges. Correlations and cluster analyses were performed using PASW, 19 (SPSS Inc., Chicago, IL, USA).

RESULTS

I recorded 1860 songs from 534 birds in 2010 and 2011 (Table 1) (“birds” here and below from 2010 are not necessarily individuals as sites were visited twice in that year). These included 199 American Pipits, 161 Wilson’s Warblers, and 174 White-crowned Sparrows (Table 1). During the first visit to survey periods in 2010, I recorded 48 American Pipits from six sites, 21 Wilson’s Warblers from four sites, and 29 White-crowned Sparrows from five sites (Table 1). I recorded 62 American Pipits, 43 Wilson’s Warblers, and 52 White-crowned Sparrows at the same sites later in the 2010 breeding season (Table 1). In 2011, I recorded

89 American Pipits from eight sites, 97 Wilson's Warblers from nine sites, and 93 White-crowned Sparrows from nine sites, from single visits to each site (Table 1). The range of distances between individuals within species within-sites during 2010 was 0.022-5.8 km for American Pipits, 0.012-2 km for Wilson Warblers, and 0.023-6.5 km for White-crowned Sparrows. In 2011, the range between individuals' within-species, within-sites was 0.033-2.5 km for American Pipits, 0.016-0.8 km for Wilson's Warbler, and 0.023-2.2 km for White-crowned Sparrows.

Mean, within-site song similarity of the American Pipit was greater than mean, across-site song similarity for four of six populations of this species during both survey periods in 2010 (Fig. 2A,B). In 2011, six of eight populations of American Pipits exhibited greater mean, within-site song similarity than mean, across-site song similarity (Fig. 2C), though this difference was marginal for four of the populations. When lumping birds across sites, within mountain ranges from 2011, two of four populations of American Pipits showed greater within-range song similarity than mean similarity across all ranges (Fig. 2D). UPGMA analysis of the 2011 data set showed no geographic structure in song divergence of American Pipits (*CPCC* = 0.773; Fig. 3). Song similarity in American Pipits did not correlate with distance between mountain ranges during either survey period in 2010 (early: $r_s = 0.368$, $P = 0.177$; late: $r_s = 0.321$, $P = 0.243$; Fig. 4A,B) or in 2011 ($r_s = 0.544$, $P = 0.314$; Fig. 4D), nor did song similarity correlate with distance between site pairs within ranges in 2011 ($r_s = 0.100$, $P = 0.873$; 4C).

There was greater mean, within-site song similarity than mean, across-site similarity for two of four populations of Wilson's Warblers in 2010 during both survey periods (Fig. 5A,B). In 2011, five of nine populations of Wilson's Warblers exhibited a greater mean, within-site song similarity than mean, across-site song similarity (Fig. 5C). Mean song similarity within mountain ranges was greater than similarity across-sites in two of four populations of Wilson's Warblers in 2011 (Fig. 5D). UPGMA analysis of Wilson's Warbler song from 2011 showed no geographic structure in song divergence of Wilson's Warblers (*CPCC* = 0.912; Fig. 6). A significant positive correlation of mean song similarity between paired sites in Wilson's Warblers and distance between mountain ranges occurred during the first survey period in 2010 ($r_s = 0.943$, $P = 0.005$; Fig. 7a), but such a relationship was not statistically evident during the second survey in 2010 ($r_s = 0.714$, $P = 0.111$; Fig. 7B) or among sites within mountain ranges in 2011 ($r_s = 0.074$, $P = 0.875$; Fig. 7C). There was a significant negative correlation between song similarity in the Wilson's Warblers and distance between mountain ranges during 2011 ($r_s = -0.99$, $P = 0.01$; Fig. 7D).

White-crowned Sparrows exhibited greater mean, within-site song similarity than, mean across-site similarity in four of five populations during both survey periods in 2010 (Fig. 8A,B), and in eight of nine sites in 2011 (Fig. 8C). Mean song similarity within mountain ranges was greater than mean similarity across all birds in two of four populations of White-crowned Sparrows during 2011 (Fig. 8D). UPGMA analysis of the 2011 data set generally clustered populations of White-crowned Sparrows within contiguous alpine habitat within mountain ranges, although, Front Range populations showed some divergence (CCPC = 0.760; Fig. 9). Song similarity was also shown across the study area where mountain ranges clustered with nearest geographic neighbors, particularly between the Front and Ten Mile ranges (Fig. 9). Mean song similarity of White-crowned Sparrows between mountain ranges did not correlate with distance between sites during the first (r_s = 0.151, P = 0.676; Fig. 10A) or second (r_s = 0.207, P = 0.567; Fig. 10B) survey periods in 2010, or in 2011 (r_s = -0.257, P = 0.623; Fig. 10D). However, there was a significant, negative correlation between mean, paired-site song similarity and distance between sites within contiguous alpine habitat, within ranges, in 2011 (r_s = -0.685, P = 0.090; Fig. 10C). Within individual, contiguous alpine zones, White-crowned Sparrow songs were most similar between the most proximate sites (a consistent pattern between the Front and Sawatch ranges).

Table 1. Distribution of research sites for each alpine species, and the sample size of birds recorded at each site during two sampling periods in 2010 (a. early season; 6/14-6/26, b. late season; 6/27-7/12), and 1 period in 2011(6/2-7/5). The corresponding number of songs recorded at each site across both years is also listed. Dashed lines represent no sample taken during that period or at that location.

Species	Mountain range and recording site	No. birds 2010 (a)	No. birds 2010 (b)	No. birds 2011	No. songs	UTM coordinates
American Pipit						
	Chicago / Mt. Evans	10	10	11	105	13S 444605 E 4382323
	Front / Mt. Sundance	9	10	---	63	13T 439712 E 4473305
	Front / Ute Trail	---	---	10	32	13T 441601 E 4470580
	Front / Rock Cut	---	---	14	50	13T 437874 E 4474018
	Front / Flat Top Mt.	---	---	10	35	13T 442623 E 4465549
	Rabbit Ears / Park Mt.	8	10	---	59	13T 403860 E 4462568
	Rampart / Pikes Peak	10	10	---	63	13S 496117 E 4299025
	Sawatch / N. Indep. Pass	6	12	10	94	13S 365380 E 4331019
	Sawatch / S. Indep. Pass	---	---	12	40	13S 363381 E 4329842
	Ten Mile / Mt. Silverheels	5	10	10	81	13S 409424 E 4357187
	Ten Mile / Red Mt.	---	---	12	38	13S 413596 E 4360600
White-crowned Sparrow						
	Chicago / Mt. Evans	6	10	10	89	13S 444605 E 4382323
	Front / Mt. Sundance	5	10	12	95	13T 439712 E 4473305

	Front / Fall River Rd.	---	---	10	35	13T 437236 E 4476900
	Front / Flat Top Mt.	---	---	7	31	13T 442623 E 4465549
	Rampart / Pikes Peak	6	10	---	52	13S 496117 E 4299025
	Sawatch / N. Indep. Pass	5	11	12	100	13S 363381 E 4329186
	Sawatch / W. Indep. Pass	---	---	10	33	13S 362279 E 4329842
	Sawtach / Willow Park	---	---	13	46	13S 367312 E 4331900
	Ten Mile / Mt. Silverheels	7	11	9	93	13S 409424 E 4357187
	Ten Mile / Alma	---	---	10	36	13S 408997 E 4353489
Wilson's Warbler						
	Chicago / Mt. Evans	5	11	10	92	13S 444605 E 4382323
	Front / Hallowill Park	---	---	15	43	13T 448344 E 4465549
	Front / Moraine Park	---	---	10	45	13T 447422 E 4465549
	Front / Horseshoe Park	6	12	12	115	13T 446383 E 4473217
	Sawatch / E. Indep. Pass	5	10	12	90	13S 364111 E 4328803
	Sawatch / W. Indep. Pass	---	---	10	35	13S 362279 E 4329842
	Sawatch / Willow park	---	---	10	36	13S 367312 E 4331900
	Ten Mile / Mt. Silverheels	5	10	8	81	13S 409424 E 4357187
	Ten Mile / Alma	---	---	10	33	13S 408997 E 4353489

Figure 1. Audiospectrograph of a White-crowned Sparrow song, and the division of the song into five phrase types.

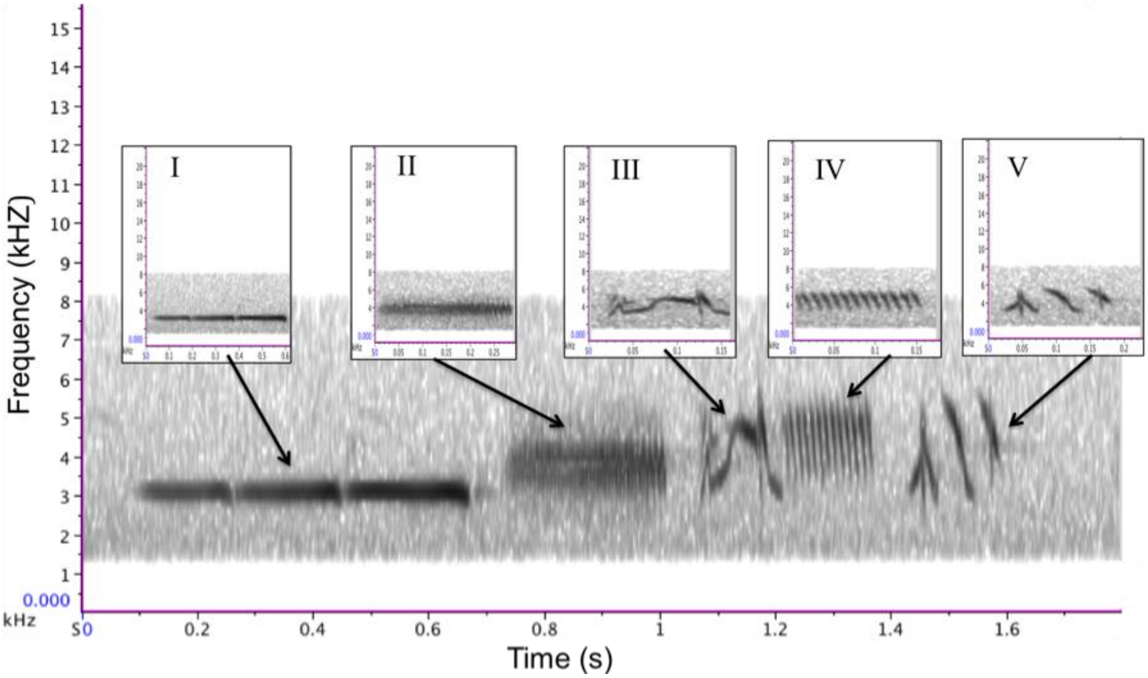

I
II
III
IV
V
Frequency (kHZ)
Time (s)
kHz
0.000
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6

Figure 2. Mean within-site song similarity (bars) versus mean similarity between birds across all sites (dashed line) for American Pipits in 2010 from two survey periods (A: 14 to 26 June, and B: 27 June to 12 July) and one survey period (2 June to 5 July) in 2011 (C:, separate recording sites, some being within the same mountain range; D: similarity within mountain ranges). Study site names are shown labeled on the *x*-axis.

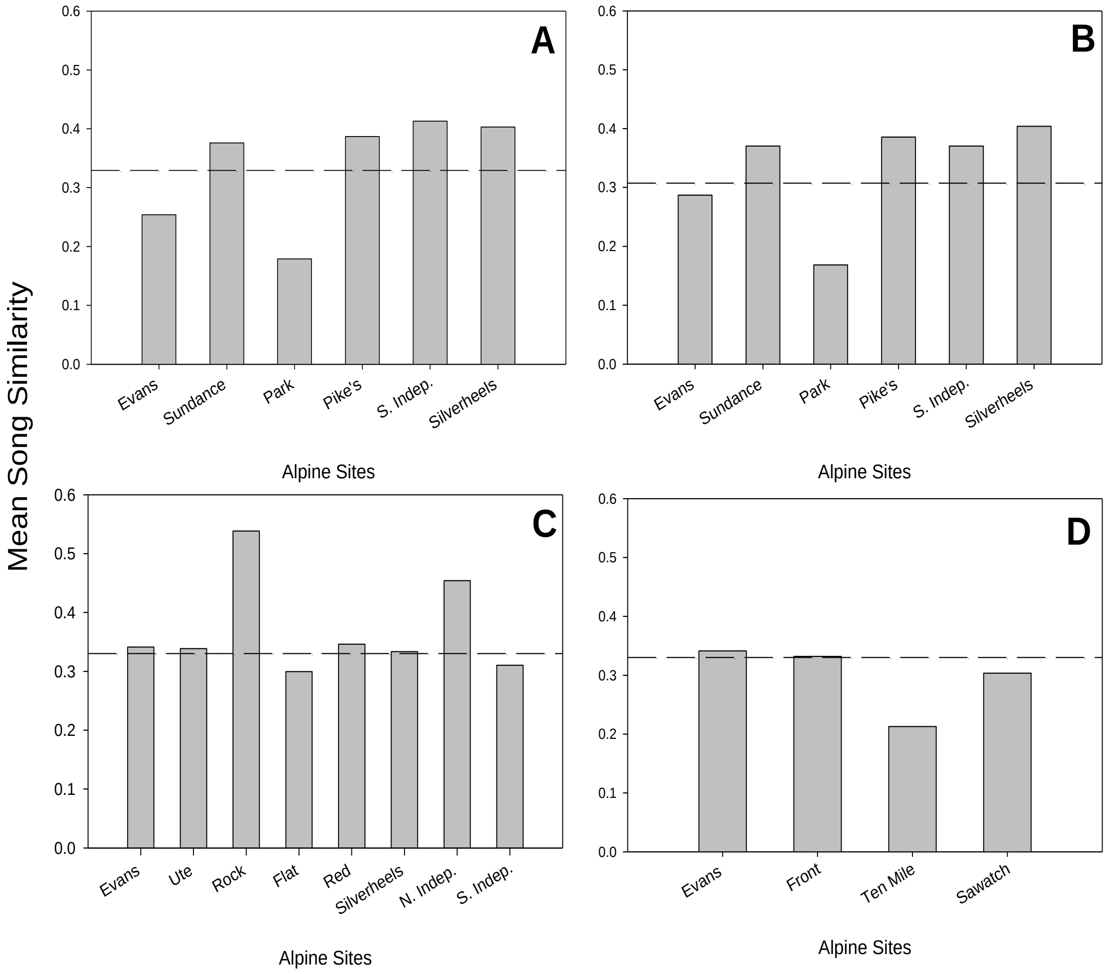

Mean Song Similarity
A
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Evans
Sundance
Park
Pike's
S. Indep.
Silverheels
Alpine Sites
B
Evans
Sundance
Park
Pike's
S. Indep.
Silverheels
Alpine Sites
C
Evans
Ute
Rock
Flat
Red
Silverheels
N. Indep.
S. Indep.
Alpine Sites
D
Evans
Front
Ten Mile
Sawatch
Alpine Sites

Figure 3. UPGMA dendrogram of song dissimilarity among American Pipit populations surveyed in 2011 (*CPCC* = 0.773). Recording sites are identified by name and mountain range association (i.e., Site.Mountain Range).

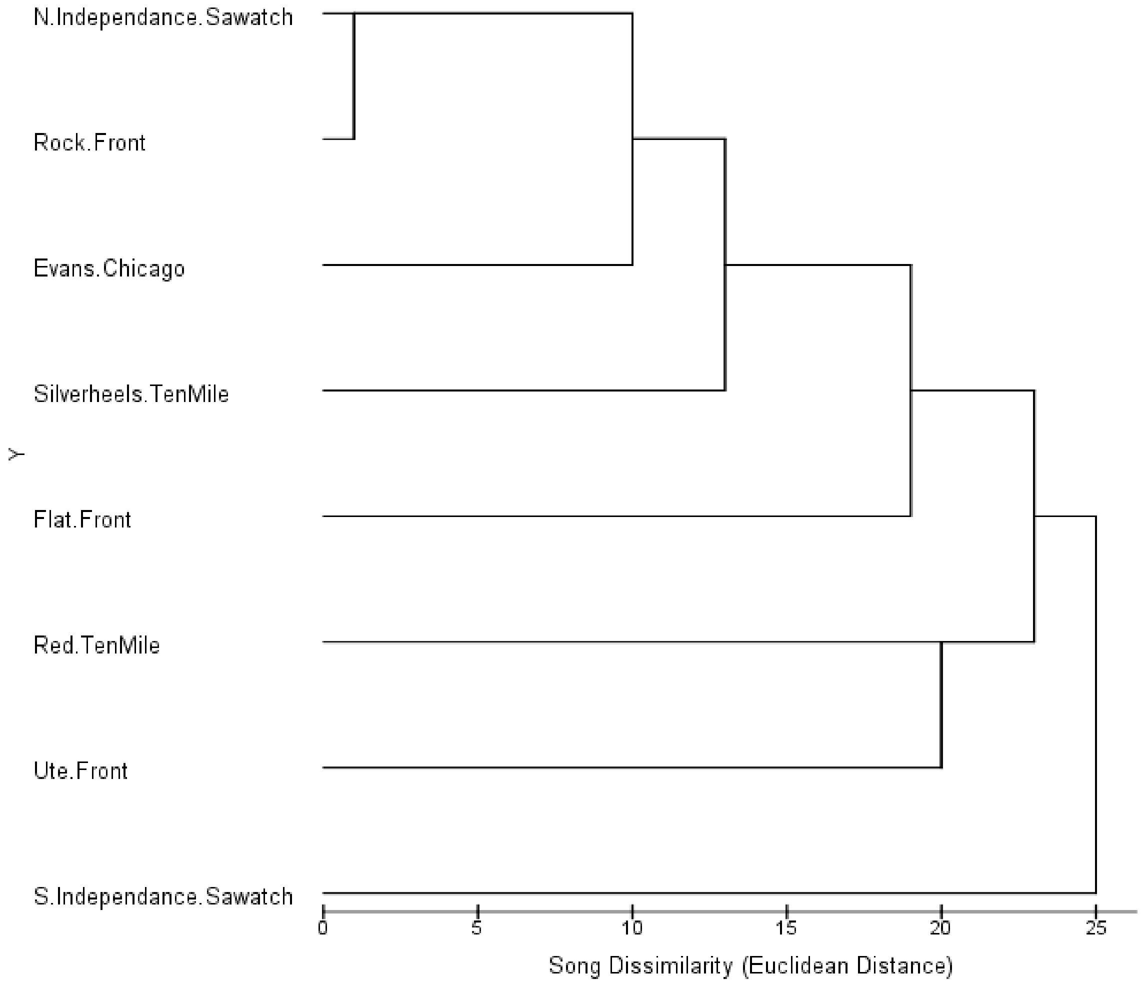

N.Independance.Sawatch
Rock.Front
Evans.Chicago
Silverheels.TenMile
Y
Flat.Front
Red.TenMile
Ute.Front
S.Independance.Sawatch
0
5
10
15
20
25
Song Dissimilarity (Euclidean Distance)

Figure 4. Mean song similarity versus geographic distance between paired sites for American Pipits during two survey periods in 2010 (A: 14 to 26 June, and B: 27 June to 12 July) and one survey period (2 June to 5 July) in 2011(C: 2011 similarity between sites within the same mountain range (closed circles denote Front Range sites, closed triangle denotes Ten Mile Range sites, closed square denotes Sawatch Range sites; D: 2011 similarity between paired mountain-range populations).

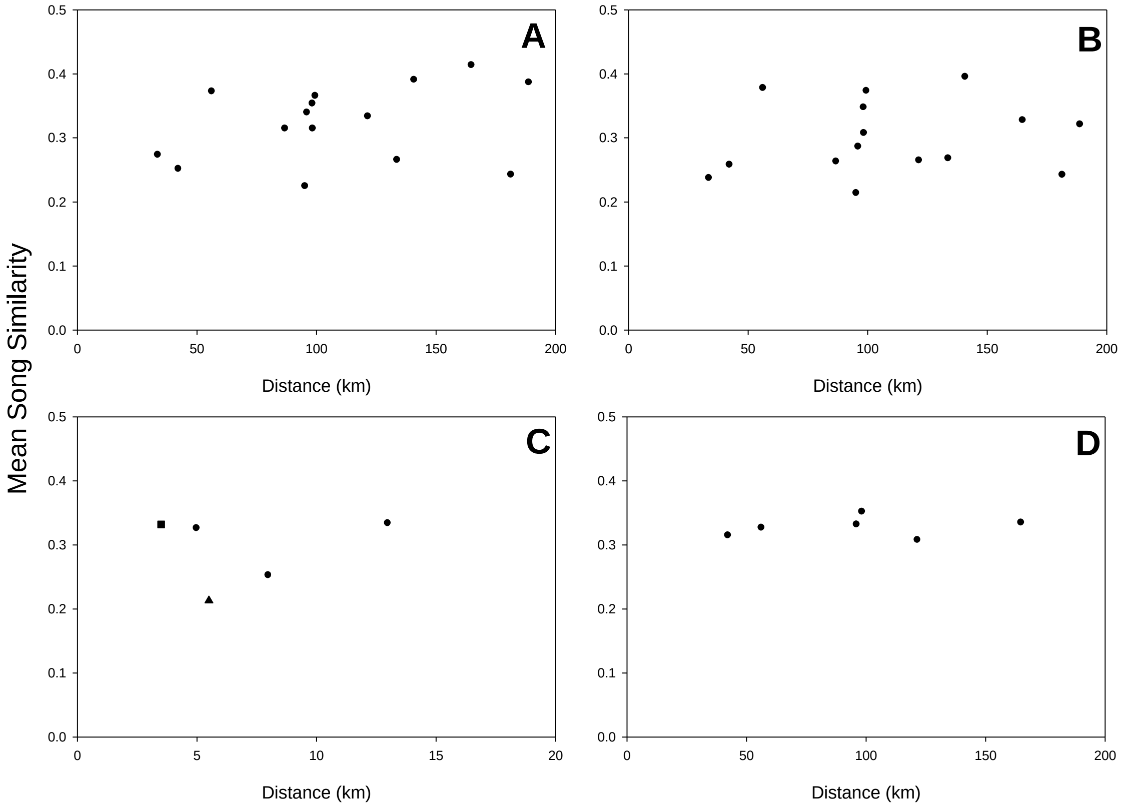

Mean Song Similarity
A
B
C
D
0.0
0.1
0.2
0.3
0.4
0.5
0
50
100
150
200
0
5
10
15
20
Distance (km)

Figure 5. Mean within-site song similarity (bars) versus mean similarity between birds across all sites (dashed line) for Wilson’s Warblers in 2010 from two survey periods (A: 14 to 26 June, and B: 27 June to 12 July) and one survey period (2 June to 5 July) in 2011 (C:, separate recording sites, some being within the same mountain range; D: similarity within mountain ranges). Study site names are shown labeled on the *x*-axis

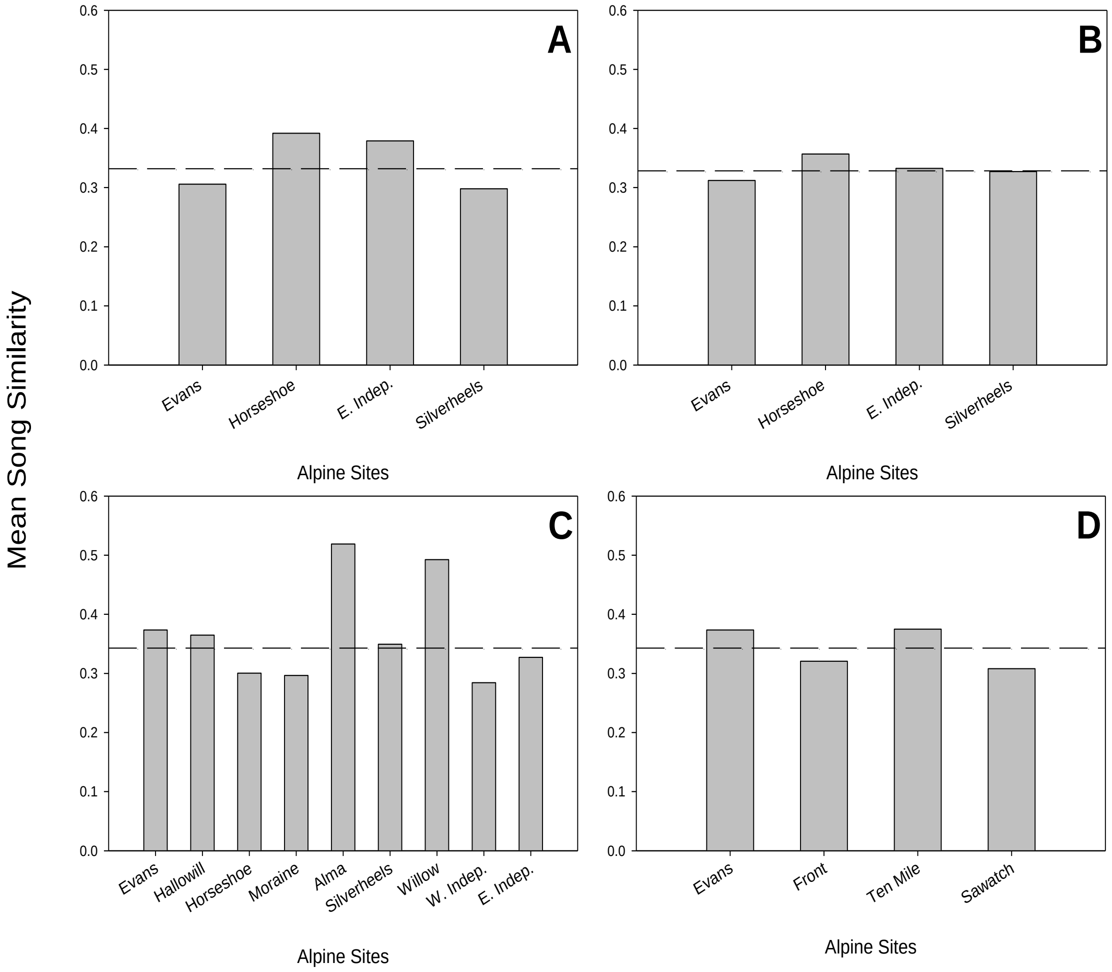

Mean Song Similarity
A
B
C
D
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Evans
Horseshoe
E. Indep.
Silverheels
Alpine Sites
Evans
Horseshoe
E. Indep.
Silverheels
Alpine Sites
Evans
Hallowill
Horseshoe
Moraine
Alma
Silverheels
Willow
W. Indep.
E. Indep.
Alpine Sites
Evans
Front
Ten Mile
Sawatch
Alpine Sites

Figure 6. UPGMA dendrogram of song dissimilarity among Wilson's Warbler populations surveyed in 2011 (*CPCC* = 0.912). Recording sites are identified by name and mountain range association (i.e., Site.Mountain Range).

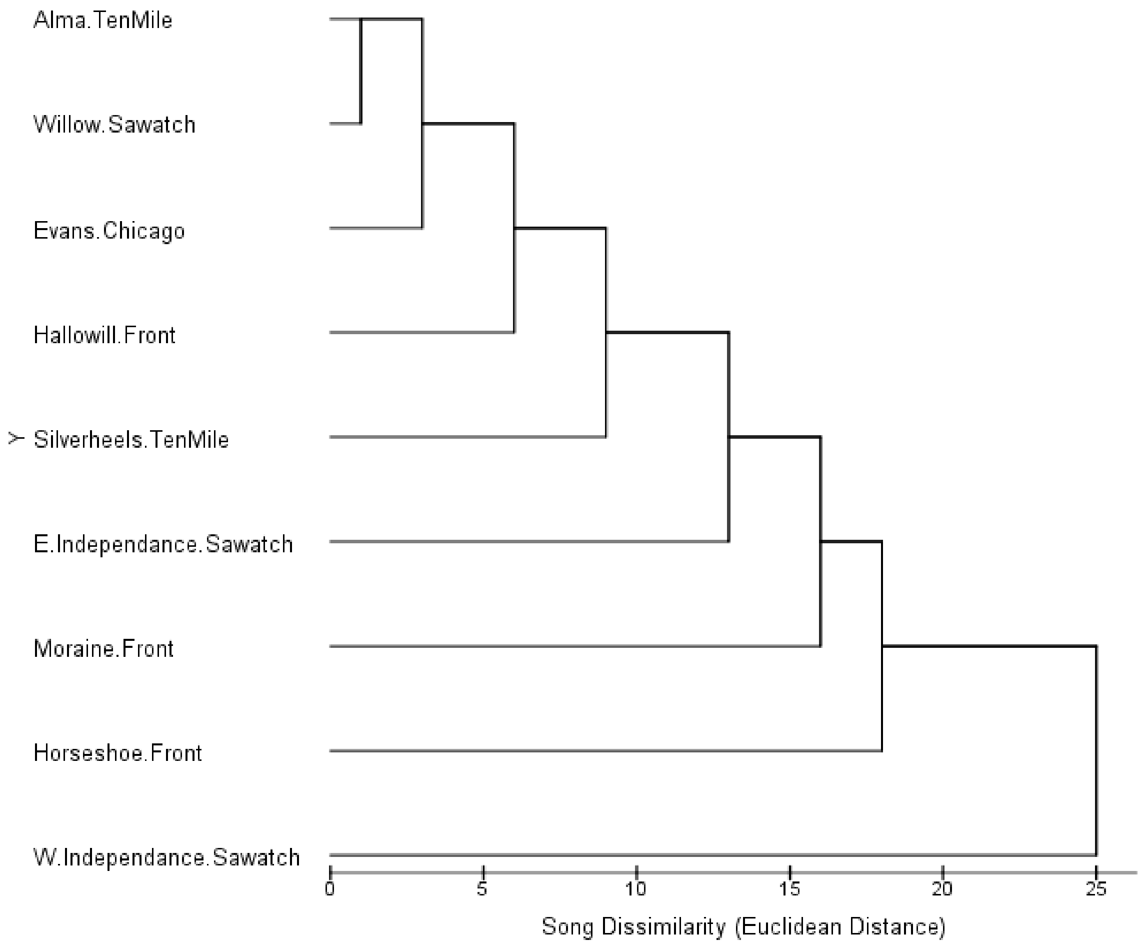

Alma.TenMile
Willow.Sawatch
Evans.Chicago
Hallowill.Front
Silverheels.TenMile
E.Independance.Sawatch
Moraine.Front
Horseshoe.Front
W.Independance.Sawatch
0
5
10
15
20
25
Song Dissimilarity (Euclidean Distance)

Figure 7. Mean song similarity versus geographic distance between paired sites for Wilsons's Warblers during two survey periods in 2010 (A: 14 to 26 June, and B: 27 June to 12 July) and one survey period (2 June to 5 July) in 2011(C: 2011 similarity between sites within the same mountain range (closed circles denote Front Range sites, closed triangle denotes Ten Mile Range sites, closed squares denote Sawatch Range sites; D: 2011 similarity between paired mountain-range populations).

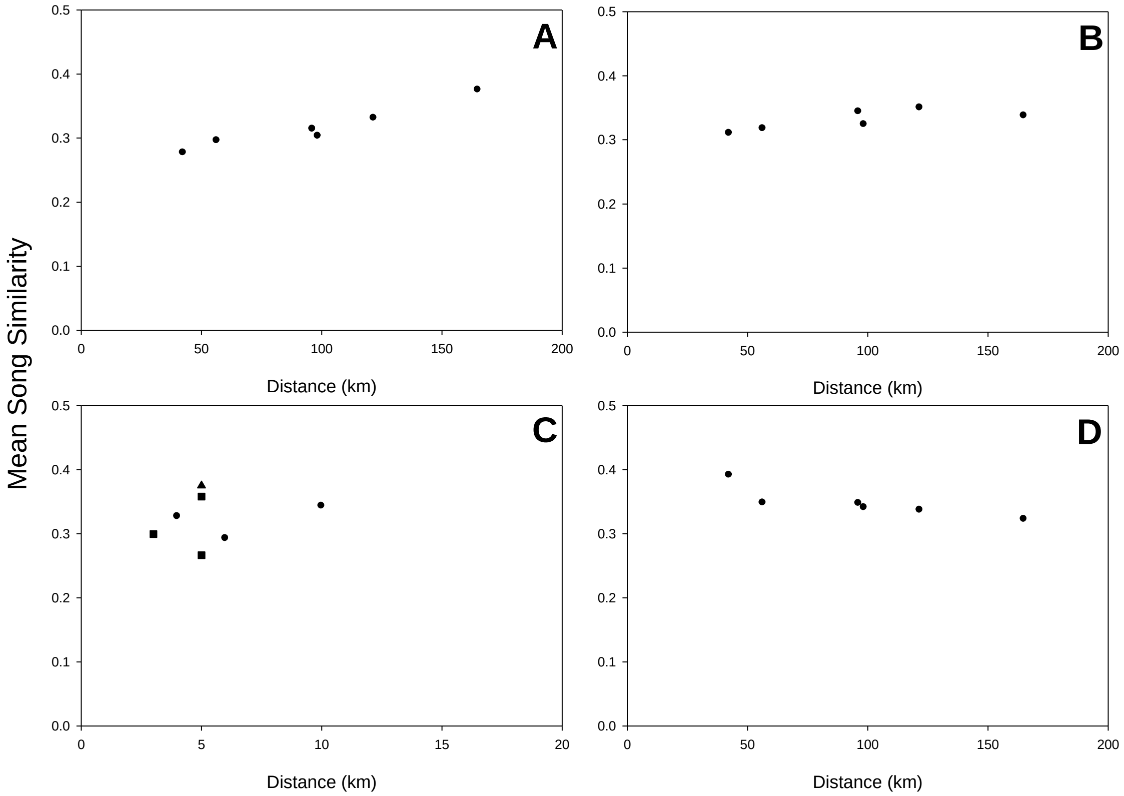

A
B
C
D
Mean Song Similarity
Distance (km)
Distance (km)
Distance (km)
Distance (km)
0.0
0.1
0.2
0.3
0.4
0.5
0
50
100
150
200
0
5
10
15
20

Figure 8. Mean within-site song similarity (bars) versus mean similarity between birds across all sites (dashed line) for White-crowned Sparrows in 2010 from two survey periods (A: 14 to 26 June, and B: 27 June to 12 July) and one survey period (2 June to 5 July) in 2011 (C:, separate recording sites, some being within the same mountain range; D: similarity within mountain ranges). Study site names are shown labeled on the *x*-axis.

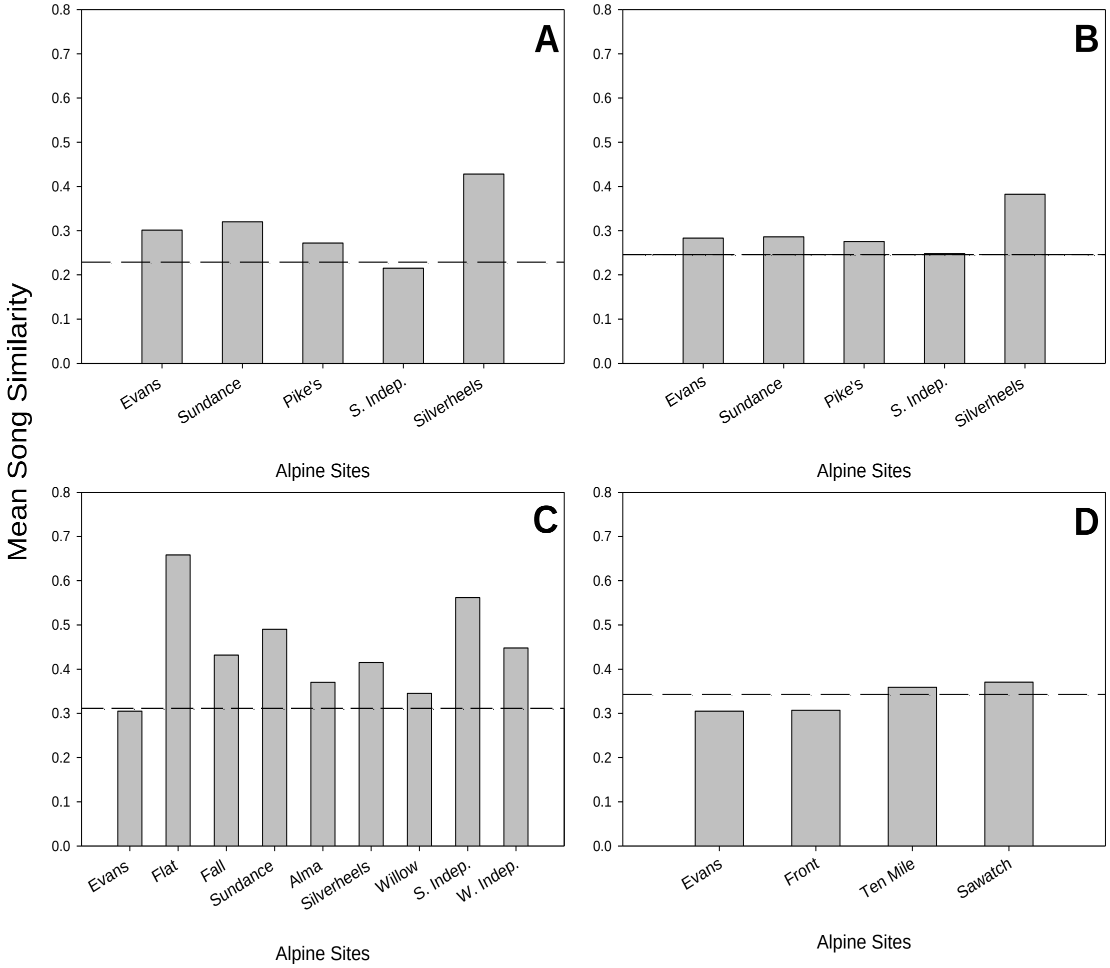

Mean Song Similarity
A
B
C
D
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Evans
Sundance
Pike's
S. Indep.
Silverheels
Flat
Fall
Alma
Willow
W. Indep.
Front
Ten Mile
Sawatch
Alpine Sites

Figure 9. UPGMA dendrogram of song dissimilarity among White-crowned Sparrows populations surveyed in 2011(*CCPC* = 0.760). Recording sites are identified by name and mountain range association (i.e., Site.Mountain Range).

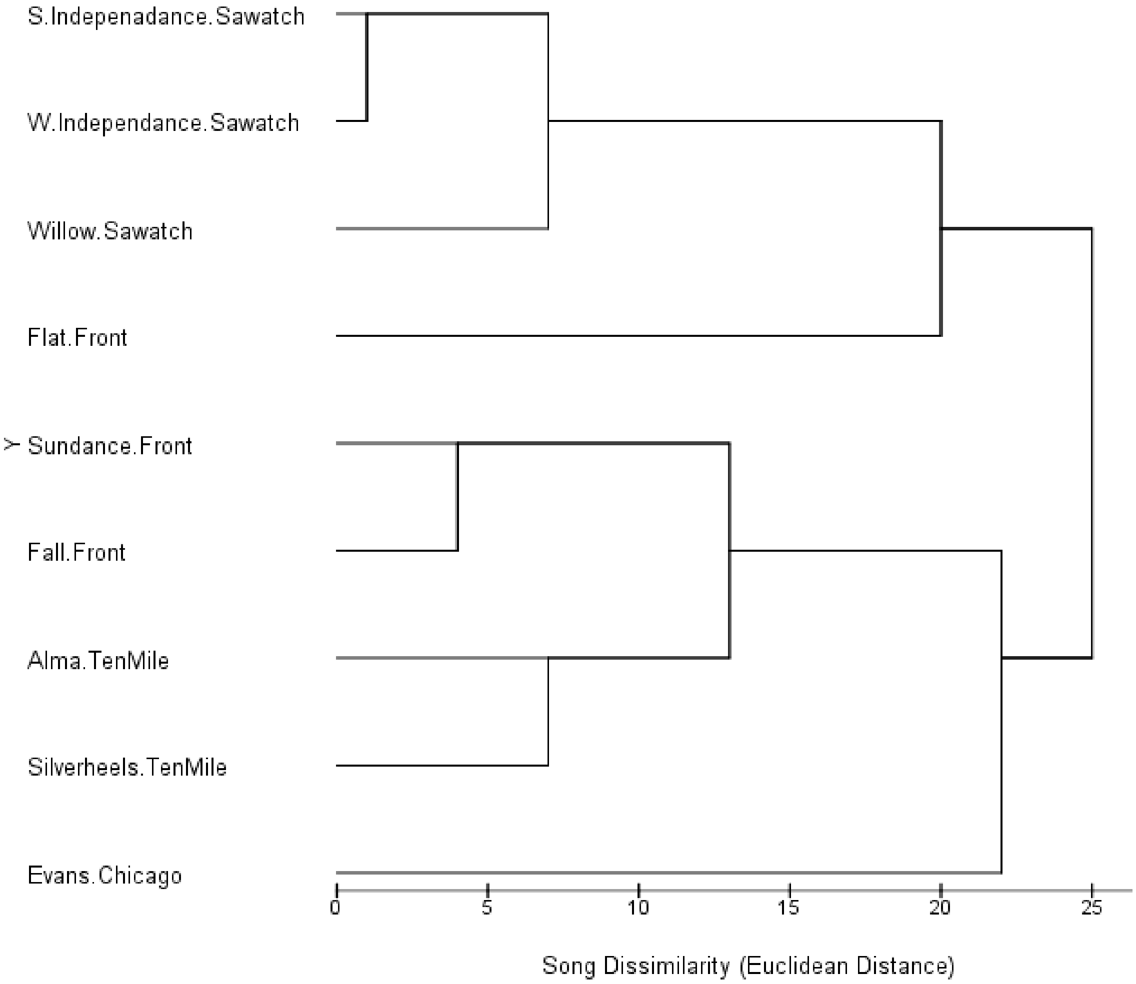
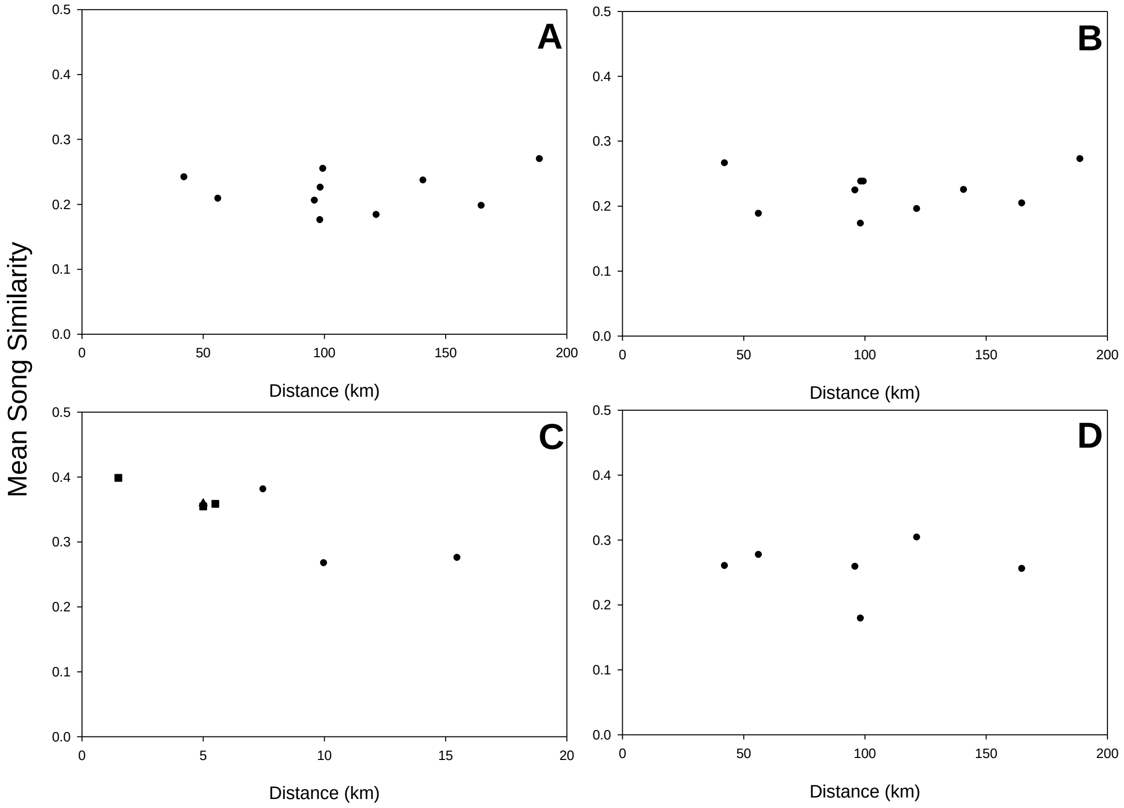

S.Indepenadance.Sawatch
W.Independance.Sawatch
Willow.Sawatch
Flat.Front
Sundance.Front
Fall.Front
Alma.TenMile
Silverheels.TenMile
Evans.Chicago
0
5
10
15
20
25
Song Dissimilarity (Euclidean Distance)

Figure 10. Mean song similarity versus geographic distance between paired sites for Wilsons's Warblers during two survey periods in 2010 (A: 14 to 26 June, and B: 27 June to 12 July) and one survey period (2 June to 5 July) in 2011(C: 2011 similarity between sites within the same mountain range (closed circles denote Front Range sites, closed triangle denotes Ten Mile Range sites, closed squares denote Sawatch Range sites; D: 2011 similarity between paired mountain-range populations).


A
B
C
D
Mean Song Similarity
Distance (km)
Distance (km)
Distance (km)
Distance (km)
0.0
0.1
0.2
0.3
0.4
0.5
0
50
100
150
200
0
5
10
15
20

DISCUSSION

I found inconsistent patterns of song divergence among alpine populations of three songbird species in the Rocky Mountains of Colorado. Song divergence was apparent, at least in some years, among alpine sub-populations of American Pipits and White-crowned Sparrows, being most evident in the latter species. Such evidence has previously been presented for Mountain White-crowned Sparrow populations, although dialects have been considered a result of categorical isolation and limited dispersal between subpopulations (Baker 1975; Orejuela and Morton 1975; Macdougal-Shackelton and Macdougal-Shackelton 2001). However, within the Colorado Rockies, dialects in White-crowned Sparrows could be explained by mere clinal variation in song with distance between individuals. Cluster analysis of White-crowned Sparrow songs from 2011 revealed distinct dialects among mountain ranges (Fig. 8), but unique dialects within ranges were evident (Fig. 7C), as was a decline in song similarity with distance between sites within mountain ranges (Fig. 9C). Therefore, dissimilarity among mountain ranges may be due to mere isolation by distance rather than any divergence of song similarity. Local dialects arising from clinal variation in song are evident in other species (Marler and Tamura 1962, Morton 1987, Cicero and Brenowitz-Fredericks 2000, Irwin 2000, Schook et al. 2008). Evidence for dialects in American Pipits during 2011 is less convincing; thus, I cannot determine if dialects in this species are related to categorical or distance isolation. I found no convincing evidence for song dialects in Rocky Mountain populations of the Wilson’s Warbler.

The majority of American Pipit populations I sampled exhibited greater within-site song similarity than across-site song similarity, though the evidence from 2010 is most convincing. This is the first description of song dialects in American Pipits; although, there have been 3 previous demonstrations of such in the *Anthus* genus (Tawney Pipit, *Anthus campestris*, Osiejuk et al. 2007; African Rock Pipit, *Anthus crenatus*, De Swardt 2010; Tree Pipit, *Anthus trivialis*, Petruskova et al. 2010). Natal dispersal in the American Pipit is not well investigated (Verbeek and Hendricks 1994); however, species that occupy landscapes that are vegetatively homogeneous (such as the alpine tundra) are expected to exhibit high rates of site fidelity (Switzer 1993), which might lead to emergence in song dialects. Although I cannot infer microgeographic song divergence from my 2011 data set, dialects observed in American Pipit songs from 2010 might resemble patterns seen in the African congener (*A. crenatus*). African Rock Pipits use a similar habitat type (montane grassland) to American Pipits and they share higher rates of songs with neighbors, although individuals separated by more than 2.2 km have dissimilar songs (De Swardt 2010). Among songbirds that sing simple repertoires (e.g., American Pipits) and exhibit limited natal dispersal, such micro-geographic song variation is common (Podos et al. 2004).

American Pipits dialects were stable across recording period dates in 2010, but dialects were substantially weaker in 2011; within-site song similarity in 2011 was only marginally greater than mean across-site similarity for four of eight sites. Additionally, mean song similarity across mountain ranges during 2011

(Fig. 1D) failed to demonstrate any pattern of dialects. Persistent winter weather (i.e., snow cover on breeding grounds) during the 2011 sampling period may have delayed territory settlement and increased inter-population dispersal and localized packing of territories in available, snow-free habitat and, thus, a more homogeneous "songscape" that year. Hendricks (2003) found that American Pipits nested later within breeding seasons when snow cover persisted longer. Additionally, inclement weather during the onset of the breeding season has commonly been shown to delay phenological development of vegetation, which acts as a cue for avian migrants to settle on territories (Ewart and Hamas 1996). White-crowned Sparrows are shrub nesters that were seen in snow-bound shrubs, apparently on territories, during the early, inclement weather in 2011 (ACD *personal observation*). Dialects in that species, unlike those of American Pipits, may, therefore, have been uninterrupted in 2011.

There was a lack of geographic structuring in song similarity of the Wilson's Warbler. Patterns of song similarity with distance between mountain ranges were evident, but these were in opposite directions between years (a positive correlation in the first survey of 2010 and a negative correlation in 2011). Homogenous patterns in song similarity are indicative of contiguous populations where song sharing may be wide-ranging (Podos et al. 2004). Previous research has documented Rocky Mountain populations of Wilson's Warblers as breeding within xeric sub-alpine meadows that are isolated by lower elevation, montane forest habitat (Finch 1989, Douglas et al. 1992, Ammon 1995). I observed a greater number of Wilson's Warblers breeding in hydrophilic riparian corridors that connect throughout valleys of the Rocky Mountains. Additionally, Wilson's Warbler populations mix during migration and on wintering grounds where the species has been observed to sing (Bent 1953; Hall 1983; Stiles and Skutch 1989; Howell and Webb 1995). Black-capped chickadees that are distributed in populations connected throughout continental North America are thought to memorize many song memes, and produce song variants that are an average of tutor models (Kroodsma et al. 1999). The songscape of Rocky Mountain Wilson's Warblers is potentially comprised of song models averaged from tutors on breeding grounds, migration, and wintering territories.

Geographic song variation in Mountain White-crowned Sparrows has been well described west of the Continental Divide (Orejuela and Morton 1975; Baptista and King 1980; Baptista and Morton 1982; Harbison et al. 1999; Macdougal-Shackelton and Macdougal-Shackelton 2001). Previous studies have reported that most Mountain White-crowned Sparrow populations exhibit local dialects (Baker 1975; Orejuela and Morton 1975; Baptista and King 1980; Macdougal-Shackelton and Macdougal-Shackelton 2001). In my study, White-crowned Sparrows generally exhibited greater song similarity within recording sites than across sites in both years of study, demonstrating stronger dialect patterns than my other two study species. However, the pattern from 2011 appeared to illustrate microgeographic divergence in song similarity among recording sites rather than exemplifying divergence of dialects among isolated alpine zones. There were 2 populations (Pike's Peak in 2010 and Mt. Evans 2011) that did not exhibit dialects (song similarity within sites was less than mean similarity across sites), which may be attributed to limited breeding habitat at those sites that can result in high turnover rates of birds and their dialect (Orejuela and Morton 1975; Harbison et al. 1999). The resemblance between my research and that of others in demonstrating dialects in the White-crowned Sparrow lends credence to my approach in detecting any dialects, should they have existed, in my other two study species.

The UPGMA cluster analysis revealed the similarity of sparrow song among sites within contiguous mountain ranges in 2011 (the Flat Top Mountain site being an exception, possibly due to the site's distance from other Front Range sites, 10–15 km). However, song similarity among mountain ranges in 2010 and 2011 did not correlate with distance between ranges. Despite our evidence for isolation by distance being a potential mechanism for divergence of alpine-defined dialects in Mountain White-crowned Sparrows, geographic barriers between isolated populations might contribute to the emergence of dialects due to limited cultural transmission among those isolates (Orejuela and Morton 1975). This may explain why my research, and work by Baptista and King (1980) found that paired-site song similarity, across mountain ranges, was not always related to distance between sites.

Despite the lack of clear evidence for clinal song variation at a range wide scale in White-crowned Sparrows, song similarity correlated with distance between recording sites within the same ranges in 2011. It is likely that the extent of distance between ranges (38-189 km) limits the resolution with which to observe clinal song variation in the White-crowned Sparrow at that scale

(Macdougal-Shackelton and Macdougal-Shackelton 2001). Male White-crowned Sparrows (*Z. l. oriantha*) typically disperse less than 2 km from natal sites (Morton 1992), and songs are modeled from tutors on natal sites and breeding grounds (Baptista and Morton 1988). Thus, song transmission is limited among individuals separated by distances such as those between ranges in my study. Based on the microgeographic patterns of White-crowned Sparrow songs within mountain ranges, divergence in songs of the White-crowned Sparrow seen among mountain ranges could be explained by distance between populations, rather than vicariant isolation of those breeding populations by impermeable barriers.

CONCLUSION

My study represents the first demonstration of dialects in American Pipits, and the first negative results for dialects in Wilson's Warblers. I further demonstrated that White-crowned Sparrow populations of Colorado Rockies resemble song-sharing patterns previously found in this species west of the Continental Divide. Song dialects in American Pipits and White-crowned Sparrows could result from population fragmentation that reduces song transmission and increases cultural mutation (Lynch 1996), but patterns from my analyses suggest that the dialects in the Rocky Mountains (at least in White-crowned Sparrows) might be a function of isolation by distance rather than geographic isolation, per se.

There were observable differences in song-sharing patterns among my three study species. My study demonstrates that elevational fragmentation of alpine habitats does not likely promote a uniform affect on cultural traditions in songbird species restricted to the alpine zone. Lamarckian processes that govern cultural transmission may explain the differences I found in song-sharing patterns among the species (Cavalli-Sforza and Feldman 1981). The proximate causes of unique song patterns among these species are likely related to differing dispersal patterns and song mutation processes (Lynch 1996). In the example of the White-crowned Sparrow, it seems evident that short distance natal-dispersal and song learning post dispersal (Baptista and Morton 1988) promotes microgeographic song variation.

The evidence for dialects in American Pipits and White-crowned sparrows is of particular interest relative to the effects of global climate change on the extent of alpine habitat (IPCC 2007). Geographic song divergence, whether through barriers to flow of cultural memes or mere clinal variation with distance, has the potential to promote reproductive isolation among populations and the eventual genetic divergence of avian species (Slabberkoorn and Smith 2002). As alpine habitats decline in size and number with global warming, so may decline the song diversity of the avian inhabitants. It follows that the simplification of such diversity could erode the potential for genetic diversification and speciation.

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Song Dialects in Alpine-breeding
Songbirds of the Rocky Mountains

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