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ORIGINAL ARTICLE

Divergence of vocal culture among isolated alpine habitats is inconsistent among three Oscine species

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Abstract Divergence in song culture has been well documented among isolated bird populations. Montane populations separated by unsuitable lower-elevation habitats thus appear to be excellent candidates for cultural divergence, and existing data support this conjecture. To explore the generality of this phenomenon, we investigated song sharing patterns in songbird species breeding in isolated alpine life zones in the Rocky Mountains of Colorado. We recorded songs of American Pipits (*Anthus rubescens alticola*), Wilson's Warblers (*Cardellina pusilla pileolata*), and White-crowned Sparrows (*Zonotrichia leucophrys leucophrys*) across 19 sites among 6 mountain ranges. We used spectrographic cross-correlation to calculate song similarity coefficients between individuals within and among populations. White-crowned Sparrows exhibited significantly elevated song sharing within isolated mountain ranges, but Wilson's Warbler and the American Pipit did not. Cluster analyses showed that White-crowned Sparrow songs diverged among alpine fragments but were generally similar among sites within contiguous alpine habitat within mountain ranges. There was no such clustering within American Pipit or Wilson's Warbler populations. Song similarity declined with distance between sites within contiguous alpine habitat in White-crowned Sparrows but not in American Pipits or Wilson's Warblers. Our results provide convincing evidence for the existence of geographically structured vocal culture in White-crowned Sparrow populations in Colorado, and this geographic pattern may be explained by clinal variation rather than by a mosaic pattern of divergence among isolated alpine fragments.

Keywords Alpine songbirds · Dialects · Rocky Mountains · Song sharing

Zusammenfassung

Kulturelle Unterschiede in den Lautäußerungen dreier Singvogelarten in isolierten alpinen Habitaten sind nicht einheitlich

Es gibt viele Belege für Unterschiede in der Gesangskultur bei isolierten Vogelpopulationen. Durch ungeeignete Tieflandhabitate voneinander getrennte Gebirgspopulationen scheinen daher hervorragende Kandidaten für kulturell bedingte Verhaltensunterschiede zu sein, und die verfügbaren Daten bestätigen diese Annahme. Um die Allgemeingültigkeit dieses Phänomens zu überprüfen, untersuchten wir die Verteilungsmuster der Strophentypen bei Singvogelarten, welche in isolierten alpinen Lebensräumen der Rocky Mountains in Colorado (USA) brüteten. An 19 Orten innerhalb von sechs Gebirgszügen nahmen wir die Gesänge von Pazifikpieper (*Anthus rubescens alticola*), Mönchswaldsänger (*Cardellina pusilla pileolata*) und Dachsammer (*Zonotrichia leucophrys*

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leucophrys) auf. Mittels spektrografischer Kreuzkorrelation berechneten wir Koeffizienten für die Gesangsähnlichkeit zwischen Individuen sowohl derselben als auch aus verschiedenen Populationen. Dachsammern zeigten innerhalb isolierter Gebirgszüge einen erheblich höheren Anteil gemeinsam genutzter Strophentypen, Mönchswaldsänger und Pazifikpieper dagegen nicht. Clusteranalysen zeigten, dass die Gesänge der Dachsammern in den alpinen Habitatfragmenten voneinander verschieden waren, sich aber gemeinhin an Orten innerhalb zusammenhängender alpiner Lebensräume ähnelten. Bei Pazifikpieper- und Mönchswaldsänger-Populationen traten solche Cluster hingegen nicht auf. Die Gesangsähnlichkeit ging bei den Dachsammern mit wachsendem Ortsabstand innerhalb zusammenhängender alpiner Lebensräume zurück, nicht aber bei Pazifikpiepern oder Mönchswaldsängern. Unsere Ergebnisse liefern überzeugende Hinweise auf die Existenz einer geografisch strukturierten Gesangskultur bei Dachsammerpopulationen in Colorado; dieses geografische Muster lässt sich eher durch klinale Variation als durch eine mosaikartige Verteilung von Unterschieden zwischen isolierten alpinen Habitatfragmenten erklären.

Introduction

Male birds sing to attract mates and deter conspecific competitors (Beecher and Brenowitz 2005). Most young oscine songbirds learn their songs by imitating nearby adults during a sensitive phase of neurological development (Catchpole and Slater 2008). Thus, birds exhibit cultural traditions, learning particular songs or song elements from conspecifics (Laland and Janik 2006; Laiolo and Tella 2007). When individuals tend to settle near their song tutors, spatial clustering of song similarity may evolve within and among bird populations (Payne 1981; Kroodsma 2004). Song divergence could result from population fragmentation that reduces song transmission and increases cultural mutation (Lynch 1996).

Researchers have commonly demonstrated spatial clustering of song similarity within—and song divergence among—songbird populations (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). Even migratory species evolve geographically structured vocal culture despite the fact that individuals have the potential to mix with individuals from other cultures at various stages of migration (e.g., Avery and Oring 1977; Payne 1982; Schook et al. 2008).

Geographic partitioning of populations appears to promote song dialect formation as exemplified by species with populations occupying oceanic islands (Newton 2003). Many species exhibit song sharing within—and divergence among—their respective island populations and the neighboring mainland (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 (Slabbekoorn and Smith 2002).

Terrestrial islands of habitat also exist within less hospitable landscape matrices, often as a result of human alteration of landscapes (MacArthur and Wilson 1967; Saunders et al. 1991). However, many habitats have historically occurred in fragmented arrays, independently from any human influence. 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 possess avifaunas distinct from the intervening valleys (Marshall 1957; Newton 2003). White-crowned Sparrow and Lincoln's Sparrow both exhibit divergence in vocal culture in populations among isolated mountaintops (Baker 1975; Orjuela 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), but these are the only two North American species studied in this regard. Song divergence among isolated alpine habitats could result from isolation, where geographical barriers (i.e., uninhabitable lowland habitats) restrict cultural transmission (Koetz et al. 2007). Alternatively, song similarity may decay with distance, as could happen within an otherwise contiguous population (Schook et al. 2008).

Our objectives were to determine if songs had diverged among bird populations breeding on isolated alpine sky islands in the Rocky Mountains of Colorado, and if so to determine the extent to which isolation versus a clinal reduction in song sharing with distance explained the patterns we observed. If isolation among mountains promoted the evolution of distinct songs, we expected to find higher levels of song sharing between pairs of birds recorded within mountain ranges than between birds recorded in different ranges. We also expected that, when we grouped sites according to similarity of song, sites from within mountain ranges would be more similar to each other than sites from different mountain ranges. If song sharing declines with distance, we expected to observe higher

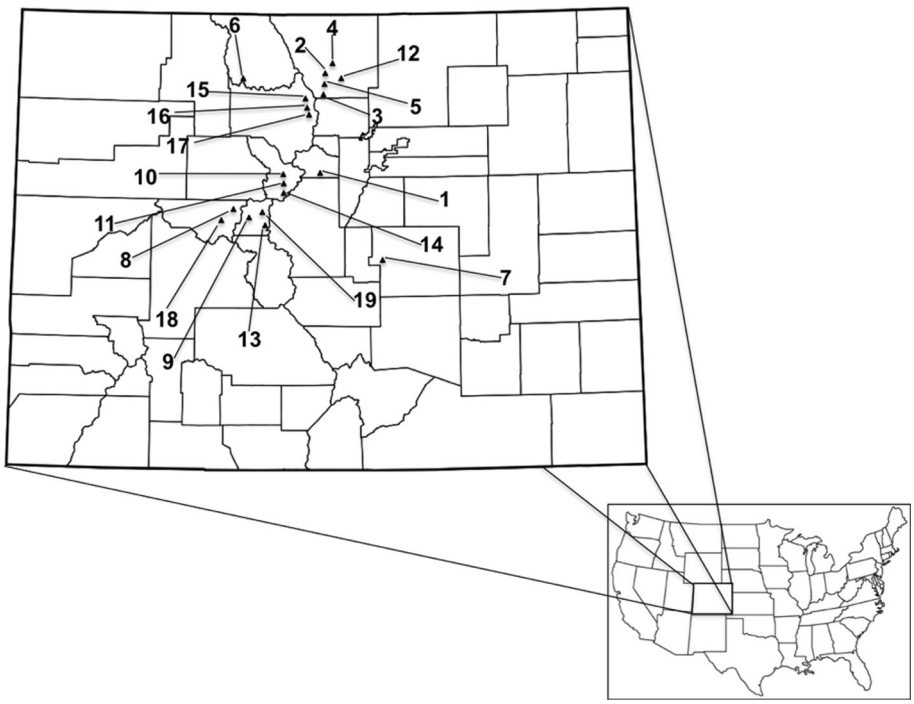

Fig. 1 Recording sites (numbers correspond to locations in Table 1) used in 2010 and 2011 to measure song sharing patterns in American Pipits (*Anthus rubescens alticola*), Wilson's Warblers (*Cardellina pusilla pileolata*), and White-crowned Sparrows (*Zonotrichia leucophrys leucophrys*)

levels of song sharing between more proximate pairs of birds recorded within contiguous alpine habitat than more distant birds within the same contiguous habitat or across mountain ranges.

Methods

Study species

We investigated alpine-breeding populations of the American Pipit (*Anthus rubescens alticola*), Wilson's Warbler (*Cardellina pusilla pileolata*), and White-crowned Sparrow. These three species (1) breed in high-elevation habitats isolated by valleys between mountain ranges (American Pipit, Verbeek and Hendricks 2012; Wilson's Warbler, Ammon and Gilbert 1999; White-crowned Sparrow, Chilton et al. 1995), (2) do not move among mountain ranges during the breeding season (American Pipit, Hendricks 1987; Wilson's Warbler, Ammon and Gilbert 1999; White-crowned Sparrow, Chilton et al. 1995), (3) tend to produce single song types per individual (American Pipit, Verbeek 1965; Wilson's Warbler, Bent 1953; White-crowned Sparrow, Marler and Tamura 1962), thus allowing characterization of songs with relatively few recordings, and (4) show moderate to high site fidelity in which adults tend to return to the same neighborhood to breed each year (Wilson's Warbler, Ammon and Gilbert 1999; White-crowned Sparrow, Chilton et al. 1995). American Pipits sing in flight, and both Wilson's Warblers and White-crowned Sparrows sing while perched. White-crowned sparrows are not open-ended learners and their songs are typically crystallized within 50 days; thus, geographic song patterning in this species is likely not due to adult imitation of songs within vocal neighborhoods (Marler 1970). Song ontogenies of the American Pipit and Wilson's Warbler have not been well investigated (Verbeek and Hendricks 2012; Ammon and Gilbert 1999).

Study area/populations

We collected data among the naturally fragmented alpine habitats of the Rocky Mountains of Colorado. Alpine habitat comprised of tundra grasses and forbs, low-lying shrubs, and granite outcroppings was fragmented by lower elevation coniferous forest. We surveyed alpine habitats that occurred between 3,500 and 4,200 m in Rocky Mountain National Park, and in the Arapaho, Medicine Bow-Routt, Pike, and San Isabel National Forests.

We recorded songs in patches of alpine habitat containing at least six singing individuals of a target species on each of six mountain ranges in 2010: Front, Rabbit Ears, Rampart, Chicago, Ten Mile, and Sawatch; and four mountain ranges in 2011: Front, Chicago, Ten Mile, and Sawatch (Fig. 1; Table 1). We recorded individuals of each target species at single locations per each mountain range in 2010 (Fig. 1; Table 1). In 2011, we used multiple (2–3) sites within contiguous alpine habitat per mountain range, spaced 3–15.5 km apart (Fig. 1; Table 1). Establishing multiple sites within discrete alpine patches allowed us to

Table 1 Distribution of research sites for each alpine species, and the sample size of American Pipits (*Anthus rubescens alticola*), Wilson's Warblers (*Cardellina pusilla pileolata*), and White-crowned Sparrows (*Zonotrichia leucophrys leucophrys*) recorded at each site during two sampling periods in 2010 (*a* early season, 14–26 June, *b* late season, 27 June–12 July), and one period in 2011 (2 June–5 July)

Species	Mountain range/recording site (ID number)	No. birds, 2010 (a)	No. birds, 2010 (b)	No. birds, 2011	UTM coordinates
American Pipit	Chicago/Mt. Evans (1)	10	10	11	13S444605, E4382323
	Front/Mt. Sundance (2)	9	10	0	13T439712, E4473305
	Front/Ute Trail (3)	–	–	10	13T441601, E4470580
	Front/Rock Cut (4)	–	–	14	13T437874, E4474018
	Front/Flat Top Mt. (5)	–	–	10	13T442623, E4465549
	Rabbit Ears/Parkview Mt. (6)	8	10	–	13T403860, E4462568
	Rampart/Pikes Peak (7)	10	10	–	13S496117, E4299025
	Sawatch/N. Indep. Pass (8)	6	12	10	13S365380, E4331019
	Sawatch/S. Indep. Pass (9)	–	–	12	13S363381, E4329842
	Ten Mile/Mt. Silverheels (10)	5	10	10	13S409424, E4357187
	Ten Mile/Red Mt. (11)	–	–	12	13S413596, E4360600
Wilson's Warbler	Chicago/Mt. Evans (1)	5	11	10	13S444605, E4382323
	Front/Hallowill Park (15)	–	–	15	13T448344, E4465549
	Front/Moraine Park (16)	–	–	10	13T447422, E4465549
	Front/Horseshoe Park (17)	6	12	12	13T446383, E4473217
	Sawatch/E. Indep. Pass (18)	5	10	12	13S364111, E4328803
	Sawatch/W. Indep. Pass (19)	–	–	10	13S362279, E4329842
	Sawatch/Willow park (13)	–	–	10	13S367312, E4331900
	Ten Mile/Mt. Silverheels (10)	5	10	8	13S409424, E4357187
	Ten Mile/Alma (14)	–	–	10	13S408997, E4353489
White-crowned Sparrow	Chicago/Mt. Evans (1)	6	10	10	13S444605, E4382323
	Front/Mt. Sundance (2)	5	10	12	13T439712, E4473305
	Front/Fall River Rd. (12)	–	–	10	13T437236, E4476900
	Front/Flat Top Mt. (5)	–	–	7	13T442623, E4465549
	Rampart/Pikes Peak (7)	6	10	–	13S496117, E4299025
	Sawatch/N. Indep. Pass (8)	5	11	12	13S363381, E4329186
	Sawatch/W. Indep. Pass (9)	–	–	10	13S362279, E4329842
	Sawatch/Willow Park (13)	–	–	13	13S367312, E4331900
	Ten Mile/Mt. Silverheels (10)	7	11	9	13S409424, E4357187
	Ten Mile/Alma (14)	–	–	10	13S408997, E4353489

Recording site identification (*ID*) numbers in parentheses correspond to geographical locations in Fig. 1

–, No sample taken during that period or at that location

determine if geographic patterning in songs was a simple clinal decay in song similarity within—and among—contiguous patches or if song types were categorically distinct within—but differed among—isolated patches. In both years, we selected mountain ranges separated by 38–189 km.

Song recording

We recorded songs daily during June and July in 2010 and 2011 after substantial snowmelt and the arrival of the study species. In 2010, we recorded at each location twice; first in mid-June (14–26 June) and again during late June/early July (27 June–12 July). Song sharing patterns remained stable through the breeding season of 2010 (see "Results"); thus, we recorded the songs of target species only once at each site in 2011 (2 June–5 July). We recorded songs using a Marantz PMD-670 compact flash recorder and a Sennheiser MKH70 long shotgun microphone $\leq$50 m from target subjects. We 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). We are confident that we sampled from an individual bird only once during a recording session by following a protocol of (1) performing all recordings during a single sampling session at each recording site

(we visited sites twice in 2010, but we analyzed these data separately as the identity of birds could not be verified between visits), (2) mapping the assumed territory of the recorded bird by following it as it sang, (3) sampling from a mapped territory only once, and (4), when possible, noting distinguishing visible marks of recorded birds. We used a global positioning system (GPS) to determine Universal Transverse Mercator (UTM) coordinates of recorded birds.

The recordings used to produce the spectrograms in Figs. 2 and 3 are available from the Animal Sound Archive at the Museum für Naturkunde Berlin (http://www.animalsoundarchive.org; see Electronic Supplementary Material).

Statistical analyses

We analyzed digital.wav sound files graphically from sound spectrograms generated in Raven Pro 1.4 (Cornell Lab of Ornithology, Ithaca, NY, USA) (Fig. 3). We used spectrographic cross-correlation (SPCC) (Clark et al. 1987; Cortopassi and Bradbury 2000; Baker and Logue 2003) to quantify similarity of songs between all possible pair-wise combinations of recorded individuals per species (Fig. 3). We used a sample rate of 48 kHz, a 256 sample Hann window, filter bandwidth of 270 Hz, time grid resolution of 128 samples with 50 % overlap, and a discrete Fourier transformation size of 256 samples (Charif et al. 2010). We used a band pass filter to eliminate noise beyond the frequency range (1,500–8,000 kHz) of birds' songs. We also filtered out other evident noise within this frequency range, making sure to avoid filtering any notes of the target bird. We initially divided songs (using Raven Pro) into like phrase types (i.e., contiguous spectrograph traces or multiple traces that were consistently found together in the same order) for pair-wise comparisons among birds within species (Figs. 2, 3). American Pipit song generally contained 1–2 phrases, Wilson's Warblers sung 1–2 phrases, and White-crowned Sparrows sung 4–5 phrases (Figs. 2, 3). White-crowned Sparrow phrases have been well described and occasionally are not sung in the same order (Orjuela and Morton 1975; Baptista and King 1980; Baptista and Morton 1982; Harbison et al. 1999; MacDougall-Shackleton and MacDougall-Shackleton 2001); thus, we used previous phrase descriptions to classify types and compared those like phrases (Figs. 2, 3). Since American Pipit and Wilson's Warbler songs have not been well investigated, we compared phrases according to the order they were sung (e.g., we compared phrase 1 of bird 1 only to phrase 1 of other birds). This was reasonable because we did not notice any obvious appearances of similar phrase types in different positions. We formulated song similarity for each pair of birds by calculating the mean of correlation coefficients generated from phrase type comparisons in SPCC (Fig. 3). We analyzed data from the 2 years separately. Within each species, we calculated mean song similarity within contiguous alpine areas per mountain range (2010 and 2011) and at particular recording sites within contiguous alpine areas and recording sites (2011).

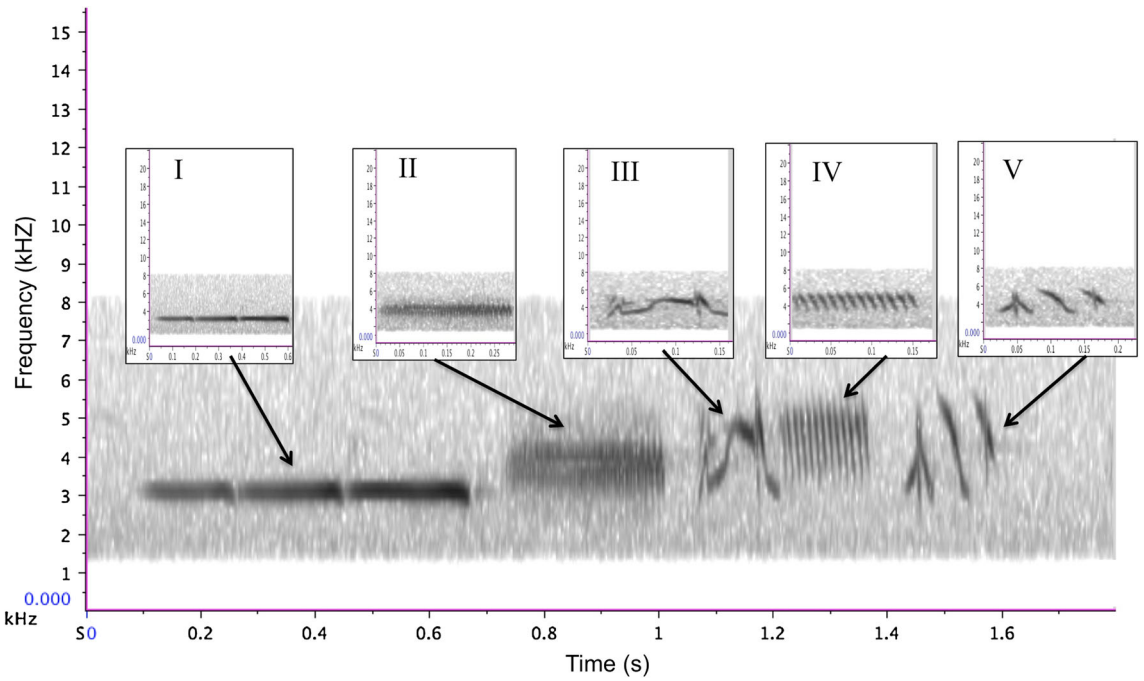

Fig. 2 Spectrogram of a White-crowned Sparrow song, and the division of the song into five phrase types

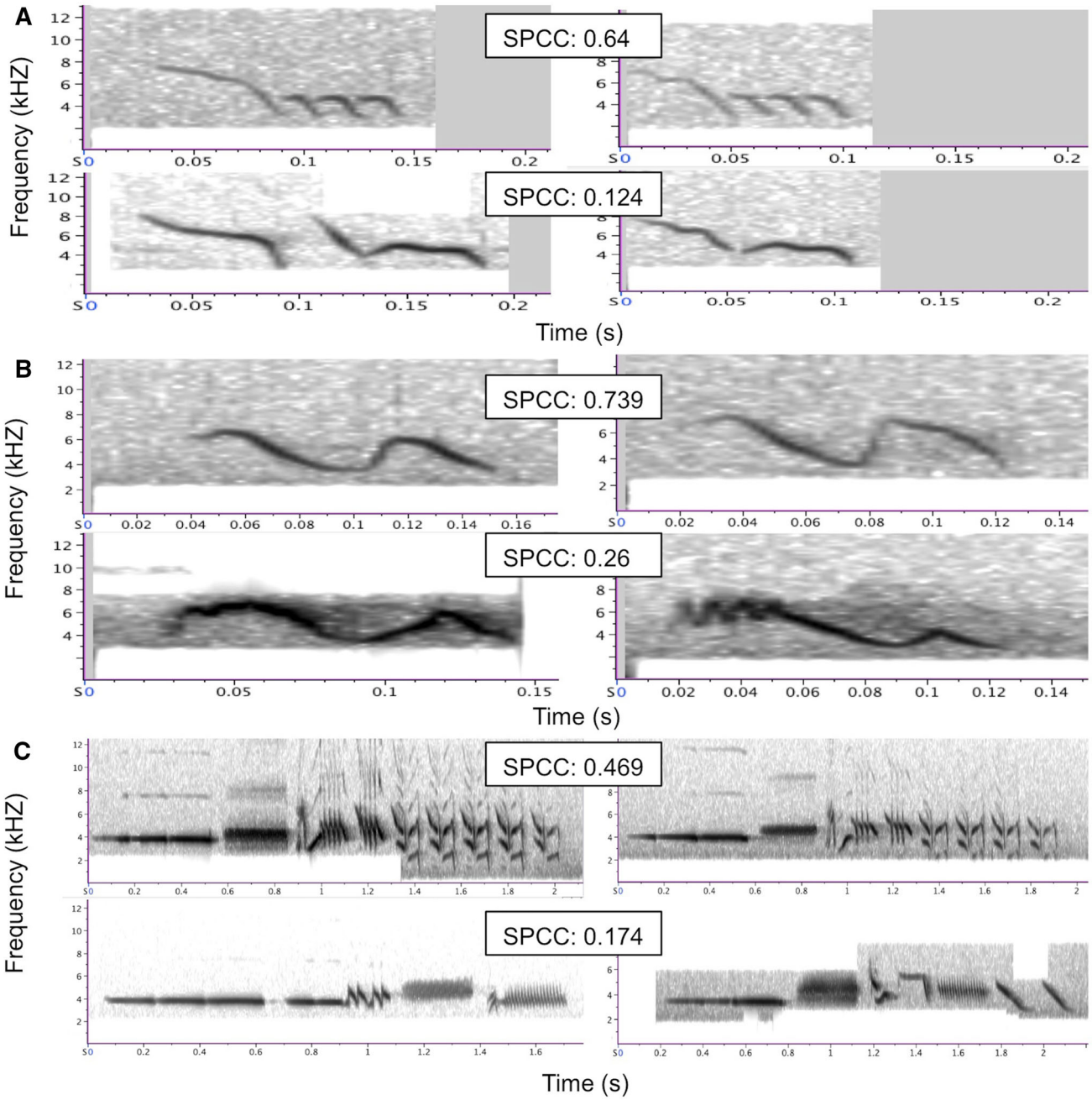

Fig. 3 Sets of song spectrograms for **a** American Pipits, **b** Wilson's Warblers, and **c** White-crowned Sparrows. The top pair of spectrograms per species represents highly correlated songs (high mean spectrographic cross-correlation, "SPCC" scores) and the bottom pair per species illustrates lesser correlated songs (lower SPCC scores) (SPCC scores were generated in Raven Pro 1.4; SPCC values are listed between paired songs). Song spectrograms from American Pipits (**a**) and Wilson's Warblers (**b**) depict individual song phrases only as individuals typically sung only one type of phrase repeatedly within a song. White-crowned Sparrow (**c**) spectrograms show entire songs comprised of five phrase types, where the SPCC values shown are mean scores across phrase types (see Fig. 2)

We wished to determine whether SPCC values for comparisons between pairs of birds tended to be higher when the two birds occupied the same site (or the same range) rather than different sites (or different ranges). We used identical methods for comparing song sharing within and among sites or within and among mountain ranges (here, we describe comparisons only among ranges for simplification, but we used identical methods to compare among sites). Because we compared each bird's song to multiple other birds' songs, comparisons were not independent and standard parametric statistical methods would generate unreliable significance tests. Our solution was to use Monte

Carlo simulations. For each set of comparisons (e.g., White-crowned Sparrow, 2011, between-mountain ranges), we first determined mean SPCC scores across all comparisons within each range and a single global mean SPCC score derived from all pairwise comparisons, both within and across ranges. We then subtracted the global mean from each within-range mean and averaged these differences. This value was the average of the extent to which sharing between birds within ranges exceeded average sharing among all birds in the analysis. This value would be positive if sharing was higher within ranges than across all pairings and negative if sharing within ranges was lower than across all pairings. To determine if a positive value was greater than would be expected by chance, we randomly shuffled all original pairwise SPCC scores. Thus, in the shuffle, each SPCC score could be assigned to any of the original ranges or as a cross-range comparison regardless of its original designation. We shuffled SPCC scores 1,000 times without replacement using the resampling option in Pop Tools v.3.2.5 (Hood 2010) in Microsoft Excel 2010 v.14 (Microsoft, Redmond, WA, USA). With each of the 1,000 sets of shuffled SPCC sores, we repeated our original calculations. If our value for the average extent to which sharing within ranges exceeded overall average sharing was larger than 95 % of the values produced by random shuffling in the Monte Carlo simulation, we concluded that song sharing within ranges was significantly higher than expected by chance.

We determined the relationship between song similarity and geographic distance in two ways. First, hierarchical UPGMA (unweighted pair group method with arithmetic mean) cluster-analysis was used on data from 2011 when multiple sites were located within contiguous alpine habitat. This analysis yielded dendrograms (Euclidean distance) illustrating divergence in song characteristics among the recorded sites. Cluster analysis output included cophenetic correlation coefficients (CPCC; i.e., correlation percentage between the distance matrix and the hierarchical transformed cophenetic matrix) that indicate how well dendrograms fit the similarity matrices from which they were derived (Sokal and Rohlf 1962). If populations isolated among islands of alpine habitat diverge in song characteristics, we expected this analysis to identify groups of recording sites within contiguous alpine patches as clusters. Second, we used Spearman rank correlation (r_s) on 2011 data to determine if mean song similarity among sites within contiguous alpine habitat on mountain ranges was related to distances between sites within those ranges. We did not assess statistical significance of the correlation analyses because our small sample size means significance is likely to result only from type I errors (Gelman and Weakliem 2009) and pairwise comparisons of birds were not independent. Instead, we cautiously interpret the sign and the size of the correlation coefficient. If song similarity declined with distance within these contiguous habitats, divergence among isolated populations might be due simply to clinal decay in song similarity with distance, rather than isolation of cultural traditions. We performed correlations and cluster analyses using PASW 19 (SPSS, Chicago, IL, USA).

Results

We recorded 1,860 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). The distances between individuals per species within-ranges (contiguous alpine habitat) during 2010 was 22 m–5.8 km for American Pipits, 12 m–2 km for Wilson Warblers, and 23 m–6.5 km for White-crowned Sparrows. In 2011, the distances between individuals within-sites was 0.033–2.500 km for American Pipits, 16 m–0.8 km for Wilson's Warbler, and 23 m–2.200 km for White-crowned Sparrows.

Mean within-mountain range song similarity of the American Pipit was greater than global mean song similarity for four of six cases during both survey periods in 2010 (Fig. 4a, b), though the overall average level of song sharing within ranges was not significantly greater than expected by chance (2010 early: $P = 0.61$; 2010 late: $P = 0.23$). In 2011, at six of eight recording sites, mean song sharing by American Pipits exceeded the global level of song sharing between all pairs of birds, and, overall, mean level of song sharing was significantly greater within recording sites than expected by chance ($P < 0.001$; Fig. 4c). This significant result appears to be driven by two sites with very high levels of song sharing as two other sites had below average sharing and the remaining four sites had mean levels of song sharing only slightly above the global mean. When lumping birds across sites within mountain ranges from 2011, three of four populations of American Pipits showed slightly higher mean within-range song similarity than mean similarity across all pairs of birds, but average within-range song sharing was not greater than expected by chance ($P = 0.35$; Fig. 2d). UPGMA analysis of the 2011 data (CPCC = 0.773) showed no geographic structure in song divergence of American Pipits among mountain ranges (Fig. 5). Song similarity in American Pipits did not negatively correlate with distance between site pairs within ranges ($r_s = 0.100$; Fig. 6a).

There was greater mean within-range song similarity than global mean similarity for only two of four populations of Wilson's Warblers in 2010 during both survey

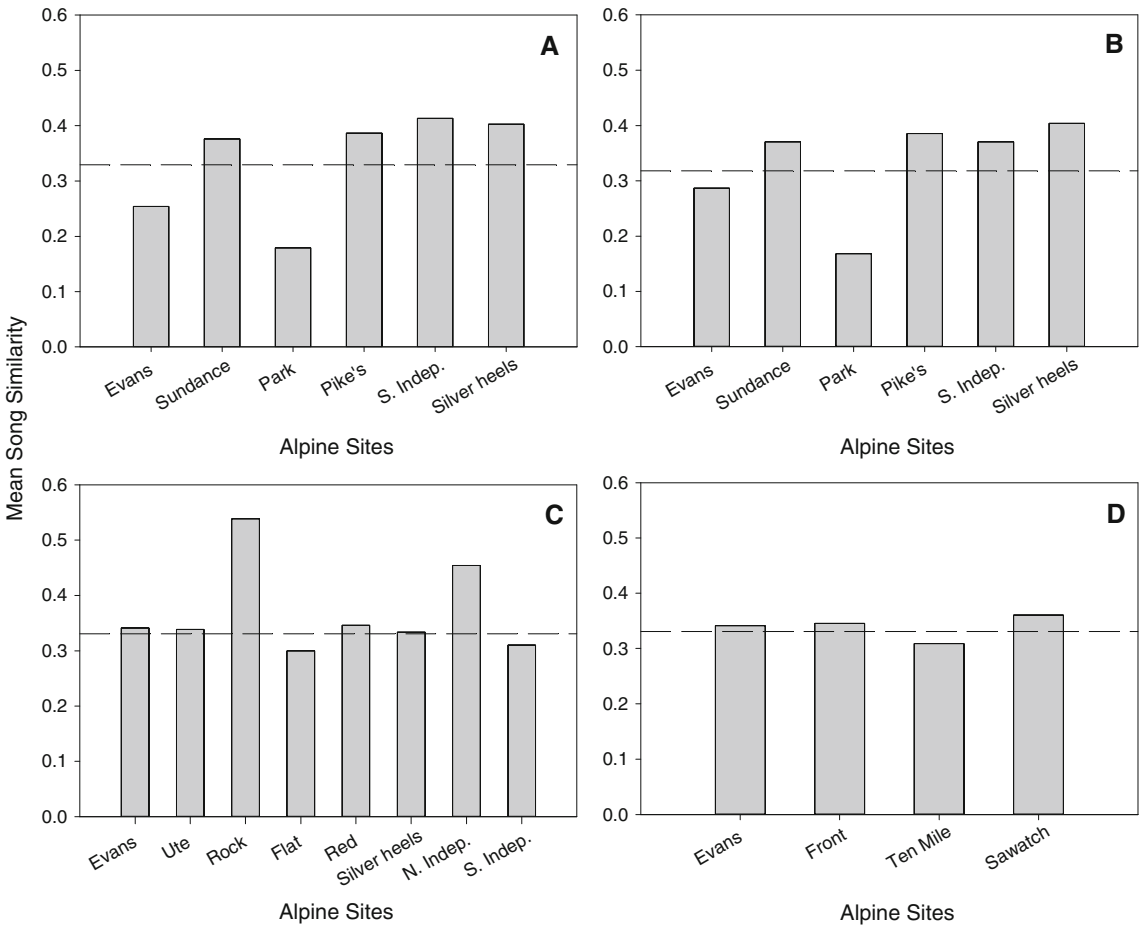

Fig. 4 Mean within-site song similarity (*bars*) versus mean similarity between birds across all sites (*dashed line*) for American Pipits in 2010 from two survey periods (**a** 14–26 June and **b** 27 June–12 July) and one survey period (2 June–5 July) in 2011 (**c** separate recording sites, some being within the same mountain range; **d** similarity within mountain ranges). Study site names are shown on the *x-axis*

periods, and not surprisingly song sharing was not statistically greater within-ranges than would be expected by chance (early: $P = 0.06$; late: $P = 0.20$; Fig. 7a, b). Despite only five of nine populations of Wilson's Warblers exhibiting a greater mean within-site song similarity than mean global song similarity in 2011, the overall mean level of song sharing within-sites was greater than expected by chance ($P < 0.001$; Fig. 7c). Mean song similarity within mountain ranges was greater than similarity between all pairs in only two of four populations of Wilson's Warblers in 2011, but overall mean similarity within-ranges was statistically greater than expected by chance ($P < 0.001$; Fig. 7d). While within-site and range-similarity during 2011 only exceeded global average sharing level on approximately half of the sites and ranges, sharing levels were very high in some of these cases and increased the overall mean level of within-site and within-range sharing. UPGMA analysis of Wilson's Warbler song from 2011 (CPCC = 0.912) showed no geographic structure in song divergence among mountain ranges (Fig. 8). Song similarity in Wilson's Warblers did not correlate negatively with distance among sites within mountain ranges ($r_s = 0.074$; Fig. 6b).

White-crowned Sparrows exhibited greater mean within-range song similarity than mean global similarity in four of five populations during the first survey period and five of five during the second period in 2010, and mean song sharing was statistically greater than expected by chance in both periods (early: $P < 0.001$; late: $P < 0.001$; Fig. 9a, b). In 2011, at eight of nine sites, mean within-site song similarity was greater than mean global similarity, and mean song sharing within-sites was greater than expected by chance ($P < 0.001$; Fig. 9c). Mean song similarity within mountain ranges was greater than mean similarity across all birds in three of four populations of White-crowned Sparrows during 2011, and average song similarity within ranges was greater than expected by chance ($P < 0.001$; Fig. 9d). UPGMA analysis of the 2011 data (CPCC = 0.760) generally clustered White-crowned Sparrow sites from within contiguous alpine habitat within

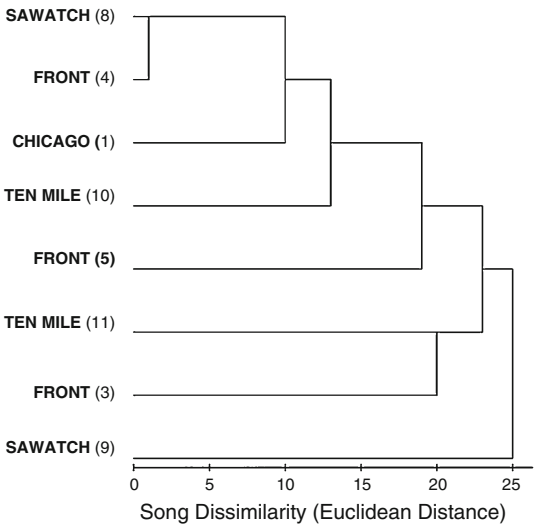

Fig. 5 UPGMA dendrogram of song dissimilarity among American Pipit populations surveyed in 2011, where there was no obvious clustering among geographically near sites (CPCC = 0.773). Recording sites are identified by mountain range association. *Site numbers in parentheses* correspond to geographical locations in Fig. 1 and Table 1

mountain ranges, although there was some divergence among recording sites in the Front Range (Fig. 10). Geographically adjacent mountain ranges (Fig. 10) also generally clustered together, particularly the Front and Ten Mile ranges (Fig. 10). We observed a moderately strong negative correlation between song similarity and distance between sites within contiguous alpine habitat within ranges ($r_s = -0.685$; Fig. 6c). In other words, within individual contiguous alpine zones, White-crowned Sparrow songs were most similar between the most proximate sites (a consistent pattern within the Front and Sawatch ranges).

Discussion

Isolation of alpine habitats did not consistently promote cultural song divergence in alpine-breeding songbird species in our study, and isolation by distance, rather than strict geographic isolation, may be sufficient to explain the patterns of cultural song divergence we observed. Of the three songbird species with populations breeding in

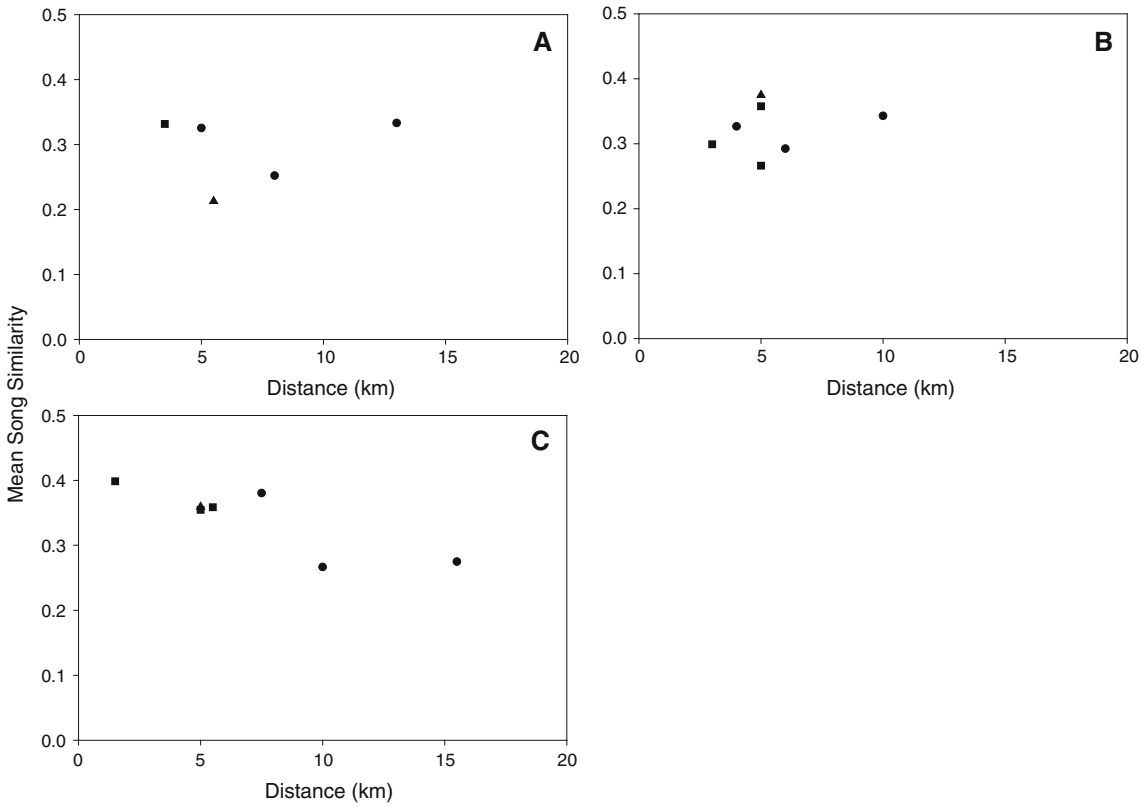

Fig. 6 Mean song similarity versus geographic distance between sites within the same mountain range (*closed circles* denote Front Range sites, *closed triangle* denotes Ten Mile Range sites, *closed squares* denote Sawatch Range sites) for American Pipits (**a**), Wilson's Warblers (**b**), and White-crowned Sparrows (**c**) during one survey period (2 June–5 July) in 2011

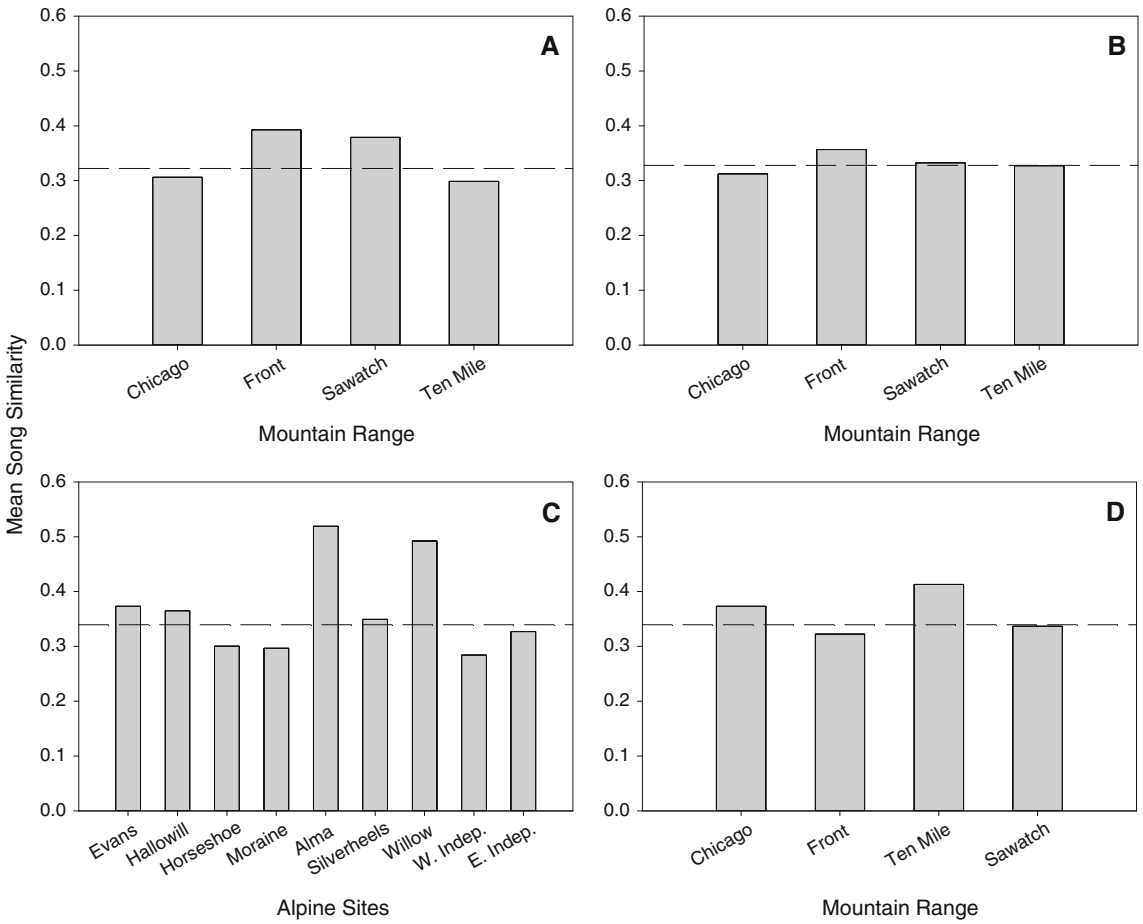

Fig. 7 Mean within-site song similarity (*bars*) versus mean similarity between birds across all sites (*dashed line*) for Wilson's Warblers in 2010 from two survey periods (**a** 14–26 June and **b** 27 June–12 July) and one survey period (2 June–5 July) in 2011 (**c** separate recording sites, some being within the same mountain range; **d** similarity within mountain ranges). Study site names are shown on the *x-axis*

isolated patches of alpine habitat, only White-crowned Sparrow showed strong evidence of song types commonly diverging among mountain ranges. White-crowned sparrows were also the only species to consistently show geographic structure in vocal culture within mountain ranges by more closely resembling within-site neighbors than conspecifics at more distant sites within the same range. However, strong song sharing within sites did occur occasionally in the other two species as well, and was strong enough in those few cases to make overall within-site sharing highly statistically significant.

Geographic song variation in Mountain White-crowned Sparrows has been well described west of the Continental Divide (Orjuela and Morton 1975; Baptista and King 1980; Baptista and Morton 1982; Harbison et al. 1999; MacDougall-Shackleton and MacDougall-Shackleton 2001), and might be due to short-distance natal dispersal or selection for local song types (Stewart and MacDougall-Shackleton 2008). In our study, White-crowned Sparrows exhibited greater song similarity within recording sites and ranges than would be expected by chance. However, in two populations (Rampart Range in 2010 and Chicago 2011), we did not detect elevated song sharing. Birds on these two sites were restricted to alpine habitat spanning only one or two mountains; starkly different from other ranges where alpine habitat was contiguous across at least ten mountains. The lack of song sharing at these sites might result from the high turnover rates of birds and their song types that are sometimes observed in small patches of breeding habitat (Orjuela and Morton 1975; Harbison et al. 1999).

Previous authors have attributed song culture divergence in Mountain White-crowned Sparrows to isolation and limited dispersal between subpopulations (Baker 1975; Orjuela and Morton 1975; MacDougall-Shackleton and MacDougall-Shackleton 2001). However, within the Colorado Rockies, we found evidence of declining similarity with distance even within contiguous habitat. Analyses of White-crowned Sparrow songs from 2011 revealed song

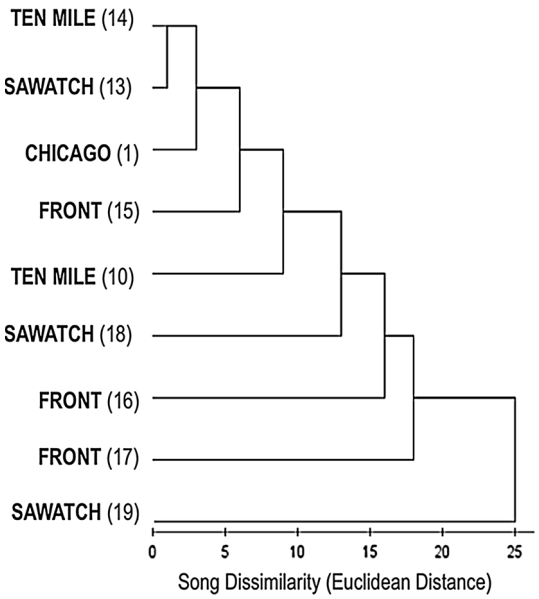

Fig. 8 UPGMA dendrogram of song dissimilarity among Wilson's Warbler populations surveyed in 2011, where there was no obvious clustering among geographically near sites (CPCC = 0.912). Recording sites are identified by mountain range association. *Site numbers in parentheses* correspond to geographical locations in Fig. 1 and Table 1

differences among mountain ranges (Fig. 9), but also differences among sites within ranges (Figs. 6c, 9). Further, song similarity declined with distance between sites within mountain ranges (Fig. 6c). However, the Flat Top Mountain site (site 5) was an exception and clustered with sites from the Sawatch Range instead of with other sites from the Front Range. This may be explained by the site's separation of 10–15 km from other Front Range sites. Male White-crowned Sparrows (*Z. l. oriantha*) typically disperse < 2 km from natal sites (Morton 1992), and songs are modeled from tutors on natal sites and breeding grounds (Marler 1970; Baptista and Morton 1988). Thus, song transmission is limited among individuals separated by distances such as those between ranges in our study, and it seems evident that short-distance natal-dispersal and/or song learning post-dispersal (Baptista and Morton 1988) promotes microgeographic song variation. However, our evidence for isolation by distance being a potential mechanism for divergence of vocal culture in Mountain White-crowned Sparrows does not preclude the possibility that geographic barriers between isolated populations contribute to the divergence of songs due to limited cultural transmission among those isolates (Orjuela and Morton 1975).

American Pipits did not exhibit greater song similarity within mountain ranges than would be expected by chance. However, we observed very high song sharing at two of eight sites within mountain ranges, and this elevated the average song sharing value above the level expected by chance (Fig. 4c). Natal dispersal in the American Pipit has not been well investigated (Verbeek and Hendricks 2012); however, species that occupy landscapes that are vegetatively homogeneous, such as alpine tundra, are expected to exhibit high rates of site fidelity (Switzer 1993) which might lead to song divergence. Closely related African Rock Pipits (*Anthus crenatus*) use a similar habitat type (montane grassland) to American Pipits and share song elements with neighbors, but 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). Although some of our pipit sites were nearly 6 km wide in 2010 and this could have reduced observed levels of sharing, they were at most 2.5 km wide in 2011 when we still failed to observe high levels of song sharing at most sites. Thus, the lack of consistent song divergence among alpine populations of the American Pipit in the Colorado Rocky Mountains is puzzling. It might be explained by persistent winter weather and late snow cover on breeding grounds of this ground-nesting species delaying territory settlement and increasing inter-population dispersal or localized packing of territories in available, snow-free habitat. Hendricks (2003) found that American Pipits initiated nesting later within breeding seasons when snow cover persisted longer. Additionally, inclement weather during the onset of the growing season delays phenological development of vegetation (Holway and Ward 1965), which acts as a cue for avian migrants to settle on territories (Ewert and Hamas 1996). Song development has not been investigated in the American Pipit (Verbeek and Hendricks 2012); however, Petruskova et al. (2010) posited that post-dispersal learning is a probable mechanism for song sharing in Tree Pipits (*Anthus trivialis*). Thus, ecological processes could temporarily mix individuals from different sites, and could lead to learning song from tutors that breed elsewhere.

There was also limited geographic structuring of song similarity in Wilson's Warbler. Significantly elevated song sharing within-sites and within-ranges in our 2011 data was driven by results from about half the sites and ranges. Previous research documented Rocky Mountain populations of Wilson's Warblers breeding within sub-alpine meadows isolated by lower elevation, montane forest habitat (Finch 1989; Douglas et al. 1992; Ammon 1995). However, we observed many Wilson's Warblers apparently breeding in riparian corridors throughout valleys between our sites. Thus, Rocky Mountain Wilson's Warbler populations are likely more connected than those of

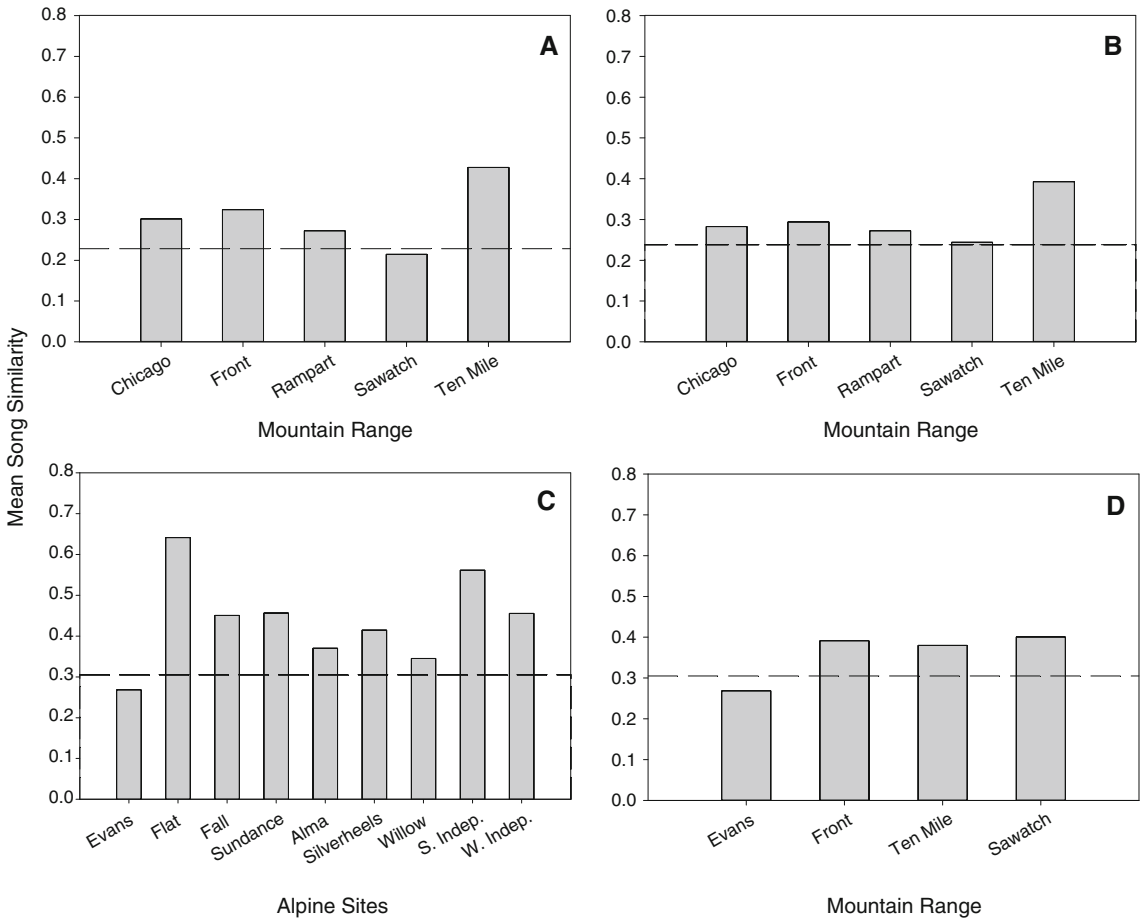

Fig. 9 Mean within-site song similarity (*bars*) versus mean similarity between birds across all sites (*dashed line*) for White-crowned Sparrows in 2010 from two survey periods (**a** 14–26 June and **b** 27 June–12 July) and one survey period (2 June–5 July) in 2011 (**c** separate recording sites, some being within the same mountain range; **d** similarity within mountain ranges). Study site names are shown on the *x-axis*

our other study species, and cultural transmission may not be limited by isolation. An absence of geographic structure in song similarity might indicate contiguous populations with song learning occurring prior to dispersal (Podos et al. 2004). Wilson's Warblers breeding in California have anecdotally been observed to return to breeding grounds with completely developed songs, although there have been no formal studies on their song development (Ammon and Gilbert 1999). Natal dispersal records show that Wilson's Warblers are rarely philopatric (3 % return rate) to natal sites in Colorado (Colorado Bird Observatory; Ammon and Gilbert 1999); thus, it seems possible that our Wilson's Warbler results may also be attributed to homogenization of songs via natal dispersal.

If species do differ in the extent to which geographic isolation or isolation by distance promotes the emergence of distinct vocal cultures, this may result from differences in selection pressures. For instance, in some species; females may prefer to mate with males singing locally common song types which might in turn select for males who learn song after dispersal or who do not disperse far from where they learn their song (Searcy and Andersson 1986). There is evidence that male Song Sparrows singing local songs also have locally adapted genotypes, and this could explain female preference for local songs (Lampe and Baker 1994; Stewart and MacDougall-Shackleton 2008). In some species, females may prefer novel sexual signals (Millington and Price 1985; Burley and Symanski 1998), and thus selection might favor males who avoid singing songs similar to their neighbors. It is also been shown that male interaction may promote song sharing by increasing territorial acquisition through reduced competition (Beecher et al. 2000). Male selection of habitats might also precipitate variations in local songs via differences in characteristics of the acoustic environment (Anderson and Conner 1985; Slabbekoorn and Smith

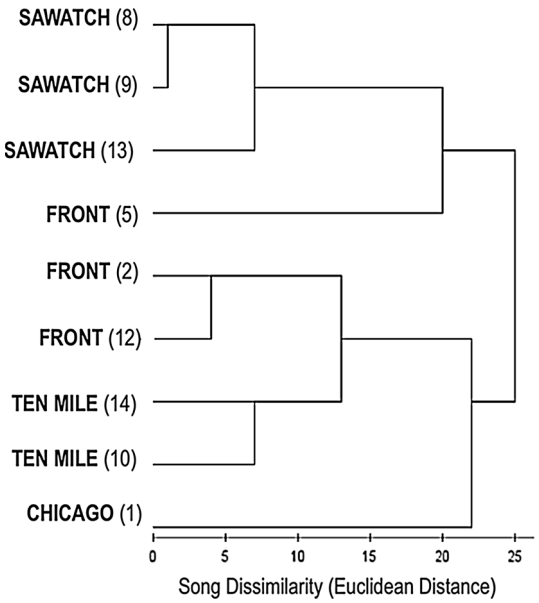

Fig. 10 UPGMA dendrogram of song dissimilarity among White-crowned Sparrows populations surveyed in 2011, where there was clear clustering among geographically near sites (CCPC = 0.760). Recording sites are identified by mountain range association. *Site numbers in parentheses* correspond to geographical locations in Fig. 1 and Table 1

2002). However, the role of such selective forces in influencing variation in vocal culture among our study species, or avian vocal culture in general, remains relatively poorly studied.

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