

Examining vesper sparrow (*Pooecetes gramineus*) songs on the National Bison Range in relation
to inter-individual distances

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Abstract

In the field of bioacoustics, the study of song is paramount in understanding how anthropogenic disturbances negatively affect bioacoustics signals, especially for conservation practices. With the decline of vesper sparrow populations in some states, limited studies on vesper sparrow songs warrant the study of their song learning strategies and song variations in order to understand associated behaviors and geographical differences. Previous studies suggest song learning occurs prior to fall migration via conspecifics. I tested to see if nearest-neighbor effects were present, whereby vesper sparrows are influenced by their neighbor songs, sounding similar to closer individuals in comparison to individuals further away. It was apparent that vesper sparrows do not learn from their neighbors but may have a preference to learn from individuals at an intermediate distance away. Songs were overall highly variable suggesting that vesper sparrows may be highly individualistic in nature and capable of invention and improvisation. Whistles appeared to follow a significant trend, though they were still highly variable amongst individuals contrary to previous studies. Vesper sparrows tutors may primarily be their fathers though other factors might have influenced the high degree of variability. Songs could be largely dependent on their post-migratory settlement or movement during breeding season, neighbors, female locality preferences, or the acoustics of the environment. Further long-term studies on contiguous, leveled grassland might better test nearest-neighbor effects. Ultimately it will also be beneficial to discover the dominant source of tutoring for fledglings in this species in order to test the plasticity of their song.

Introduction

Vocal culture can be broadly defined as the vocal repertoires of song transmitted from one generation to another over time. This evolution and transmittance of song as a cultural attribute is highly common in oscine passerines (Baptista and Schuchmann 1990) though it has also been observed in marine mammals (Baker et al. 2011) and apes (Bluff et al 2010). These acoustic signals have been found to vary between subspecies (Nelson 2000, Lopez et al. 2013), individuals (Bluff et al. 2010, Bradbury 2001), and populations (Parker et al. 2012), forming dialects unique to individuals and populations. As these dialects are socially transmitted over time, this becomes a cultural “trait” that is associated with a particular population.

Typically, vocal learning of song in birds involves young males imitating older males or neighboring conspecifics (Nelson 2000), although there may be innate or genetic predispositions towards a particular song (Nelson 2000). The mechanisms of vocal evolution however are not completely understood and songs have been suggested to change in response to female preferences on song features, male competition, maladaptive hybridization, morphological plasticity or constraints and changing environmental conditions affecting vocal transmission (Xing et al. 2013). Geographic variation of song and dialects have been well studied among passerines (Derryberry 2011, Bradbury et al. 2001, Kleeman et. Al, 2005, Eilers and Slabbekoorn, 2002) and continues to be crucial as studies have indicated the possibility of song variation as a pathway to speciation (Ripmeester et al. 2009, Xing et al. 2013). With the identification of such geographical variations in song, evolutionary histories of a species can be deciphered, as well as a better understanding of the driving factors behind vocal dialect and vocal cultures. As vocal culture is influenced by the changing physical environment (Baker 2011, Ortega et al. 2014) this warrants in-depth study to ensure conservation of novel species as well as

the unique habitats that they originate from as often times the acoustics of song mirror the acoustic properties of these habitats (Baker 2011).

Increasing evidence indicates that anthropogenic disturbances negatively impact bioacoustic signals of mammals, amphibians, fishes and birds (Laiola. P 2010). Such alterations in acoustic signals of organisms and consequently behavior and population dynamics, have suggested bioacoustics as an effective tool for conservation management (Laiola. P 2010). Previous studies have shown the importance of bird song as a potential bioindicator of diversity and identifying populations in decline (Laiolo et al. 2008) due to the alteration of song in response to urban development (Patricelli and Blickley 2006, Katti and Warren 2004). Knowledge and study of birdsong dialects should provide insight into restoration and management practices as birdsong and bioacoustics as a whole are easily measured (Laiola. P 2010).

Geographic variability of bird song is often affected by the environment, which influences the acoustic properties of song such as amplitude, frequency, duration of song, rate of delivery, timing of songs (Lopez et al. 2013, Bolus 2014) to that which optimally suits the habitat, a process known as the acoustic adaptation hypothesis (Bolus 2014, Morton 1975, Derryberry 2009). Over time it can be assumed that songs or even components of songs evolve differently in response to differences in ecological or environmental pressures within a certain habitat. Forests, for example create a great hindrance to sound propagation due to dense vegetation (Blumenrath and Dabelsteen, 2005, Mathevon et al. 2005). Additionally, when vocalizing across long distances or in the presence of noise, frequencies have been observed to vary to maximize transmission. (Mathevon et al. 2005, Williams et al. 2012). Coupled with geographical distribution and habitat characteristics, distance is also a factor influencing the

vocal variability and formation of dialects. It has been commonly agreed on that oscine passerines that are found in the same area are prone to have a higher degree of similarity in comparison to their distant individuals (Schook et al. 2008). This has been observed in the Dickcissel (*Spiza americana*) (Schook et al. 2008), California House Finches (*Carpodacus mexicanus*) (Bitterbaum and Baptista 1979) and Great Tits (*Parus major*) (Rivera-Gutierrez et al. 2010). This pattern however appears to be species specific as sage sparrow individuals showed greater similarities in song with distant conspecifics in comparison to their immediate neighbors (Wiens 1982).

Vesper sparrows are considered a threatened species in certain states (Colorado Division of Wildlife 2005) and are prone to population declines due to land use changes (Jones and Cornely 2002) habitat loss, fragmentation and particularly cattle grazing (Bock et al. 1993, Kantrud and Kologski 1982). Conversely, mixed results in one study question the effects of grazing on vesper sparrows as bird abundance was not affected despite cattle grazing on vegetation preferred by vesper sparrows (Harrison et al. 2010). Their song however has been understudied, and there is limited understanding of their vocal culture due to the high degree of song variability (Kroodsma 1972). Additionally their life history with regards to the initiation of song learning remains unclear to the best of my knowledge. Kroodsma (1972) and Ritchison (1982) seem to suggest learning of songs (syllables) or components of their song before migration in the fall leading me to believe the same occurs on the bison range. Kroodsma (1972) also suggests that conspecifics play a large part in tutoring.

While their introductory notes are considered to be fairly consistent, dialects for these syllables were observed whilst the rest of the song remains highly variable (Kroodsma 1972). Conversely, another study concluded that no dialects were observed though the highly variable

nature of their song was also noticeable (Ritchison 1981). Ritchison (1981) also suggests that the vesper sparrow may be highly individualistic, sharing very few syllables of their song and possessing highly exclusive song patterns though there were some exceptions of shared syllables. Both studies were conducted in Oregon and Minnesota respectively, suggesting that geographical differences may also influence the formation of dialects and degree of variability. To the best of my knowledge, no studies concerning the vocal culture or song-learning strategies of vesper sparrows have been conducted in Western Montana, including the National Bison Range.

The objective of this study was to examine whether vocal variation in vesper sparrow song correlates with increasing distances between individuals using a song-sharing decay curve (Fig. 1). This model infers that birds tend to learn from their neighbors, that is imitating or improvising one another and sharing elements of their song that may lead to a higher degree of similarity observed between neighbors (i.e. closest individual). Learning may occur via social learning, involving social interaction and transmission of song or song elements from one bird to another; or self-learning, which includes methods of invention, improvisation and the early stages of learning 1st year vesper sparrows may undergo. From this, I would be able to determine if the similarity of songs between individuals decreases as distance increases. Additionally, this would allow me to investigate the absence or presence of vocal dialects. I hypothesize that the overall pattern observed from this sample of vesper sparrow recordings from the National Bison Range to follow the song-sharing decay curve as (Fig. 1). Due to a high degree of individuality and territoriality, variability between neighbors and distant conspecifics is also expected, but similarities should also be notable due to the shared geographic location of these individuals and former research indicating consistent introductory notes (Kroodsma 1972, Ritchison 1981).

Methods

Study Site

Recordings of vesper sparrows were all conducted on the National Bison Range (NBR), Moiese MT. As an important breeding ground for grassland birds, the National Bison Range is an essential ecosystem that provides various habitats contributing to grassland bird diversity. Since the rise of agricultural practices in the 1800s and consequent fragmentation and loss of native plant communities, the National Bison Range has become one of the few remaining areas of conserved palouse prairie (Looney and Eigenbrode 2012).

A total of 36 transects were carried out in the following areas: Prairie Drive, Red Sleep Mountain Drive (NBR loop), West loop, Trisky, Pauline, “Backroad to Triangle” Trail, “Trail opposite Triangle”, “Backroad into NBR”, Tower 2, and Tower 1. No recordings were obtained from Tower 1, Tower 2 (Fig. 7).

Recordings, Transects, and Mapping

Each transect was 1 mile in length with the exception of transects 144, 188, and 198. This was due to the transect reaching a dead end or an impassable end (e.g. outskirts of the bison range adjacent to the highway). When prime vesper habitat was observed to disappear along certain transects or vesper sparrows were no longer heard, the specific transect was cut short but the recordings obtained were included in the analyses. At each transect, when a vesper sparrow was encountered, GPS coordinates and a recording was taken. It was also noted which side of the road the sparrow was on. A recording of each individual was then conducted for a proportion of time that allowed for a minimum of 3 clear songs to be sung by the individual. This increased the chances of reproducing adequate sonograms. As not every vesper sparrow was recordable due to

noise (traffic, construction, other avian songs) total abundance for each transect was recorded. If there were two nearby individuals singing simultaneously, the recorder would say “him” after the completion of each song to distinguish between the two singing individuals. Some recordings were discarded due to the overlap of song with noise, background noise, or the inability to produce a clear sonogram during analyses. Time of the day was noted for every recording. Distance of transects, between transects and the distance between individuals was recorded and marked using a Garmin eTrex Legend H GPS device. All 60 recordings were conducted on wildlife acoustics SM2+ Song meter attached with a SMX-II weatherproof acoustic microphone. Recordings were taken between 6:00am and 12:00pm from June - Aug 2014.

Songs were then analyzed holistically for overall similarities and differences using Raven Pro 1.4 and Raven Pro 1.5. For every song, each element of song was cross-correlated against each other after being clipped from the song and saved as a WAV. file. Elements were categorized as whistles, sissels, dicksissels, or trills (Fig. 8) Trills were separated into 3 separate folders due to the inability of Raven Pro to perform batch analysis with the large number of trills. Difficulty experienced in hearing certain elements of a song was aided by slowing down the rate of song or by temporary amplification in Raven. Batch analysis was conducted across the various landscapes and with every bird pair song element to assess similarity. Jaccard Index scores were calculated by taking the sum of cross correlation values of every element and dividing by the count of all the cross correlation values. Distance for every bird pair was calculated using latitude and longitude GPS coordinates processed through the formula

$$[=ACOS(COS(RADIANS(90-LAT1))*COS(RADIANS(90-LAT2))+SIN(RADIANS(90-LAT1))*SIN(RADIANS(90-LAT2))*COS(RADIANS(LONG1-LONG2)))*6731 Km]$$
 (adapted from BLUEMM unpublished, Veness 2014, Pearson Software Consulting 2011). This formula

was also tested against a package in R known as Imap as comparison and to check for accuracy. Results were then fitted against the song-sharing decay curve (Jaccard Index Vs. distance) graph per element and for the entire song in R. Initial plotting produced graphs that appeared highly cluttered and difficult to interpret, so distance was broken down into intervals of 50 and the Jaccard Index score means calculated and clumped in accordance to the intervals. 50 intervals were chosen as it produced a more representable visualization of the data and after experimentation with the maximum number of intervals R could produce to optimize analysis and data interpretation.

For mapping and visualization of the geographic spread of similarity, bird pairs were ranked in order of descending Jaccard index values. Every bird was then separated into 5 different families based on the bird pairs sorted in descending order of Jaccard's Index. Each family was then assigned a color with Red, Blue, Green, Yellow and Brown with "Red birds" having the highest Jaccard index scores and "Brown birds" having the lowest Jaccard Index values. This was mapped out using Google maps to visualize the distribution of similarity with reference to distance.

Statistical analyses

Regression analysis and model testing was conducted by testing a log function against the Jaccards Index vs. distance graphs. This was done to test against the model based on Figure 1. Based on the scatter of the data, a polynomial regression was also conducted in an attempt to find the best fit for the data spread. All statistical analysis was conducted using R.

Results

Looking at the vesper sparrow songs as a whole, the data did not fit Jaccard's index song-sharing logarithmic decay curve significantly (Fig. 2; adjusted multiple $R^2 = 0.03107$, $P = 0.0639$). Breaking songs into their elements did not produce significance when the data was fitted to Jaccard's index song-sharing logarithmic decay curve (Fig 3A-3D). Whistles did not have a significant fit (Fig. 3A; adjusted multiple $R^2 = 0.05162$, $P = 0.06147$), Trills did not have significant fit (Fig. 3B; adjusted multiple $R^2 = -0.01077$, $P = 0.4928$), Sissels did not have a significant fit (Fig. 3C; adjusted multiple $R^2 = -0.008911$, $P = 0.455$), and Dicksissels did not have a significant fit (Fig. 3D] (adjusted multiple $R^2 = -0.009699$, $P = 0.4704$).

Polynomial regression analysis for Jaccard index versus distance of vesper sparrow songs as a whole was significant (Fig. 4; adjusted multiple $R^2 = 0.1709$, $P = 0.004587$). Polynomial regression analysis with each element had significance with whistles only (Fig. 5A; adjusted multiple $R^2 = 0.2117$, $P = 0.001403$). Non-linear regressions between Jaccard's Index and distance between birds was not significant for trills (Fig. 5B; adjusted multiple $R^2 = 0.1322$, $P = 0.01342$), Sissels (Fig. 5C; adjusted multiple $R^2 = 0.107$, $P = 0.02626$), and Dicksissels (Fig. 5D; adjusted multiple $R^2 = 0.04217$, $P = 0.1364$).

Discussion

From this sample of vesper sparrows recorded and analyzed, results indicate vesper sparrows on the National Bison Range do not learn from their neighbors, or sound similar to their neighbors, contrary to my hypothesis. Individuals closer together did not have similar songs, which would be expected if these species did learn songs from their neighbors (Fig. 1).

This can also be seen as individuals began to form large clusters as Jaccard index decreases [See Figure 6]. The contrary trend is also most notable as the whistles [see Figure 3A], supposedly the most conserved element in the vesper sparrow song (Kroodsma 1972), appeared to be highly variable and unpredictable between neighbors. However, it does appear that to some extent the distribution of data follows the model in that at the greatest distances apart, there is a high degree of dissimilarity and a high degree of similarity for those at a small distance apart (i.e. neighbors) based on the data points found at both extremes of the graphs [see Figures 2-5].

When the data for the entire songs are fitted against a polynomial regression, significance is observed [see Figures 4-5A]. However it is important to note distance only explained 17% [adjusted multiple $R^2 = 0.1709$] of the variation in Jaccard index values when looking at the songs holistically, and 21% [adjusted multiple $R^2 = 0.2117$] of the Jaccard index scores for the whistles. As the parabolic curve follows a steep decline from an intermediate distance to the greatest distance, particularly for the whistles [see Figure 5A] this indicates that as distance between birds increases, similarity in song decreases. The relationship between Jaccard's Index and distance for trills, dicksissels and sissels appeared to be approaching significance [see Figure 5B-D] when fitted against a polynomial function as compared to when they were tested for a logarithmic regression analysis [see Figures 3A-D]. Overall this suggests that bird pairs that are separated by an intermediate distance have the highest degree of similarity in song and that they do not learn from their neighbors or sound similar to them.

One hypothesis for this the high degree of similarity at intermediate distances apart may be due to the fact that vesper sparrows prefer to learn from individuals found further away. One study on Chaffinches showed that individuals preferred to learn from individuals that were 500-600m away (Lachlan and Slater 2003). This has also been observed in nightingales where the

closest neighbor is not the preferential model of imitation (Hultsch and Todt 1981). Such behavior may be rooted in that sounding like your neighbor does not provide a competitive advantage when competing for mates. For example male sedge warblers with more sophisticated songs attracted females at a faster rate (Catchpole 1987). Thus singing uniquely and elaborately may be advantageous for male vesper sparrows when trying to outcompete the nearest neighbor. This would be possible if song sharing occurred across a fair distance, in this case approximately 5 km away.

Another possible explanation for the greatest similarity found between bird pairs separated by intermediate distances may be due to the fact that vesper sparrows primarily learn songs from their fathers and may maintain this learned song after fledging. This is one of the well-known mechanisms of early song learning and has been observed in a multitude of species such as the fairy wren (Greig et al. 2012), white crowned-sparrow (Baptista and Petrinovich 1986) and the zebra finch (Hauber et al. 2010). As vesper sparrows generally do not return to the same breeding grounds (Kroodsma 1972) and have a high rate of dispersal from their breeding grounds (Ritchison 1981), these birds may have been related and tutored by the same father, explaining this geographic spread of similarity at intermediate distances. Thus this trend of that song sharing in vesper sparrows may be a reflection on natal dispersal patterns. No study on father vesper sparrows as the primary tutors have been conducted to the best of my knowledge. Controlled laboratory tutor-tutee tests would provide insight to the main preference of vesper sparrow fledglings and test the plasticity of their song to reveal other influences on song development and learning.

Age effects may have also influenced our results in that young vesper sparrows may have been recorded and included in our analysis. 1st-year males, males that fledged the previous year,

may have not established a territory and be moving between territories singing natal songs. This may occur as young males typically arrive later at their breeding grounds (Cezary Mitrus 2007) and often may not have an established territory or have successfully obtained a mate. Combined with the possibility of fledglings learning from their fathers and a high dispersal rate from their natal grounds, this may have produced the trend where greatest similarity was observed for bird pairs found at an intermediate distance from one another. Displacement into other “song populations” or territories with different song variations have been observed in vesper sparrows (Ritchison 1981) and may have confounded overall results.

Failure to fit the logarithmic decay curve suggests that overall this population of vesper sparrows may be performing individualistically and variably. Ritchison (1981) proposed that vesper sparrows were highly individualistic in song while Kroodsma (1972) concurred, mentioning in his study the highly variable nature of their songs. Kroodsma (1972) was able to detect 43 different trills in one individual vesper sparrow (Kroodsma 1972) postulating that individuals have extensive vocal variability in their song, which can be unpredictable from one individual to the next. This is supported by Ritchinson’s (1981) study on a small sample of 25 vesper sparrows that shared very few syllables (Ritchison 1981). Such behavior as exhibited with vesper sparrows on the bison range may be a result of several other song-learning strategies that may lead to highly exclusive and variable songs. This includes improvisation and invention (Beecher and Brenowitz 2005), which allows the development of novel, untraceable songs. Such is the case of Northern sedge wrens, when tutored with a playback call, choose to invent and improvise rather than learn the tutor song (Kroodsma 1999). Vesper sparrows would therefore have highly personal vocal signatures with very few shared elements though imitation may still be occurring but be sung in the same order or altered in minute ways.

What appeared to be fairly consistent however were the whistles as they were the main method of identifying individuals when we failed to spot them in the field or when incomplete songs were being recorded and analyzed. This was observed in a previous study whereby whistles were the most conserved element of vesper sparrow songs sampled (Kroodsma 1972). This can be supported to an extent as whistles had a significant fit when Jaccard index scores and distance between each bird was tested against a polynomial regression analysis (Fig.5A). As the most conserved element, they were expected to follow a particular trend and have an overall greater Jaccard index scores. However, consistent conservancy would suggest a linear regression trend with a slope close to 0 due to a high rate of conservancy no matter how great the distance apart between each bird. In addition every bird recorded had a whistle as compared to trills, sissels and dicksissels, which were highly variable. Failure of the whistles to significantly fit a logarithmic function suggests that even whistles are not learned from their neighbors but with such high conservancy, this may imply genetic predisposal as part of their song-learning mechanism or great learning accuracy if songs are learnt from their fathers. Genetic predisposal for song learning has been observed in Chaffinches whereby alterations to chromosomes produced pitch changes in bird song (Mundinger and Lahti 2014). The same genetic mechanisms may influence the conservancy and consistency of whistles in vesper sparrows, in a sense that whistles are found in every song, but may still be open to variation.

Migratory effects may have been influencing our results overall, especially if adult vesper sparrows prefer not to return to the same breeding grounds (Kroodsma 1972) and may have shared similar songs or maintained the same song during previous years. This suggests the trend observed is largely dependent on the territories and breeding grounds selected by individuals' post-migration or during the breeding season. Considering the counter-nature of vesper sparrows

to learn from their neighbors, this may explain why greater similarities were observed for individuals separated at an intermediate distance. 1st-year indigo buntings were observed to maintain their songs after migrating back to their breeding grounds but when settling into new neighborhoods, were observed to change their songs (Payne et al. 1988). A slightly similar behavior may be in effect whereby vesper sparrows, while not learning from their neighbors *per se*, may still be influenced and inventing counter-songs based off their neighbors. Their songs would therefore be constantly changing and be dependent on their neighbor, not for imitation purposes but to ensure songs are distinctive. This may be beneficial if their goal is produce unique vocal signatures since by constantly changing your breeding grounds and territories, one would have to ensure plasticity in song as you are constantly uncertain about your potential competitors, female locality preferences, and possible obstructions to song transmission. This may be why similarities were low between nearest neighbors and for distant neighbors as distance would not be a primary driving force behind song creation and differences, but who your neighbor is and what kind of repertoire is possessed by that individual, female preference and the acoustics of the environment.

Other movement patterns during the breeding season may convolute results and create random trends. Northern populations of sedge wrens are known to be migratory and semi-nomadic during the breeding season, resulting in atypical species song as they improvise and invent songs due to their constantly changing neighbors (Kroodsma 1999). While vesper sparrow breeding movements and nomadic behavior has yet to be studied in depth, this may be occurring on the National Bison Range due to competition for the relatively small area of prime habitat and that vesper sparrows are highly specific with regards to habitat preference (personal observation). Additionally territory turn-over may occur throughout the breeding season with

song changes coinciding with these movements due to novel habitat features, environmental factors, which may even include new neighbors as described earlier. On the National Bison Range, causes of territory turnover may often be due to grazing disturbances by large grazers such as bison, which are moved between pastures regularly (U.S. Fish and Wildlife, unpublished). Territory abandonment has been linked to nesting success, with lower return rates to areas of poor nesting success (Weatherhead and Boak 1986) so this may be another factor influencing movements on vesper sparrows. The songs they produce could also be a result of the females encountered in these movements as they move between territories. However confirmation of within-year territory abandonment would require long-term studies and banding of birds that was not conducted for this investigation.

One final reason for the observed variation and trends may arise from the differences in densities between areas sampled and the lack of homogenous landscape. The National Bison Range though small in nature, still has various habitats that are not all ideal for vesper sparrows. This would result in different densities of vesper sparrows being sampled at different areas, as densities appeared to be dependent on elevation, habitat availability and large, contiguous, leveled grassland habitat was really only found in 2 areas along Red Sleep Mountain Drive (personal observation). Vesper sparrows appeared to avoid forest edges, riparian areas as we saw a decline in their numbers and songs. Comparisons made between pairs found at different localities with a difference in density may have not allowed for optimal study of nearest neighbor effects on song learning. Theoretical models and past studies have shown that habitat gaps result in a decline in shared songs (Lynch and Baker 1994 and Slabbekoorn 2003), which may be case due to the lack of contiguous grassland habitat for vesper sparrows on the bison range. Habitat and microhabitat features may have influenced variations in songs and elements in accordance

but was not recorded as part of our study. Future study may focus on observing vegetative characteristics that might influence vesper sparrow density in order to conduct a similar study on contiguous grassland to observe for nearest-neighbor song learning strategies.

Based on the collective of results and hypotheses, this leads me to believe that the presence of dialects is highly probably on the National Bison Range. This is supported by the observance of a high degree of distinctiveness and variation in individual songs. Furthermore, dispersal patterns post-breeding season coupled with possible movements during the breeding season appear to favour the formation of dialects as moving into new areas may necessitate learning new songs or song variations to meet female locality or outcompete males in the preexisting area. This however remains inconclusive, and future study of National Bison Range vesper sparrows dialects must be tested in long-term studies with the use of playback calls and an analysis of counter-singing responses to decipher repertoire differences. Analysis of song over time will ensure encompassing entire repertoires, should they exist, song development and song-learning strategies of individuals as this appeared to be the key difference between existing vesper sparrow song studies that had discrepancies over the existence of dialects (Kroodsma 1973 and Ritchison 1981). Some birds may have chosen to sing different songs from their repertoire while they were being recorded so identification of entire repertoires and analysis of every song in an individuals repertoire may shed light on song sharing on the bison range. Due to their breeding dispersal patterns (Kroodsma 1972), banding birds to observe migration and breeding movement patterns may also allow us to understand vesper sparrows interaction with neighbors and the effect of song variability when colonizing new breeding areas. The variability between individuals concurs with song studies conducted in Oregon and Minneosta, implying that perhaps geographical patterns may have little effect on the variability of the vesper sparrow

song, and that the species may be innately or genetically variable in song. Conversely “dialects” may be inappropriate to classify the song repertoires of vesper sparrows on the National Bison Range if they are not geographically constrained and undergo different territories changes in the new breeding season or during the current breeding season, as it is difficult to map the occurrences and changes of these vocal signatures.

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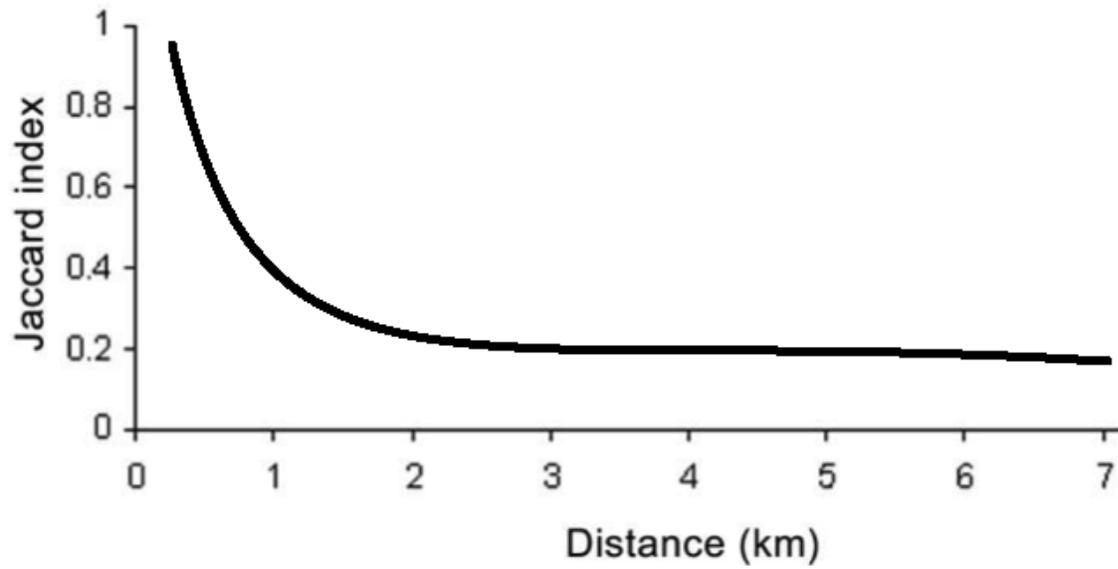


Figure 1. Song-sharing decay curve (Adapted from Schook et al. 2008)

Vesper Sparrow Song Sharing Decay Curve

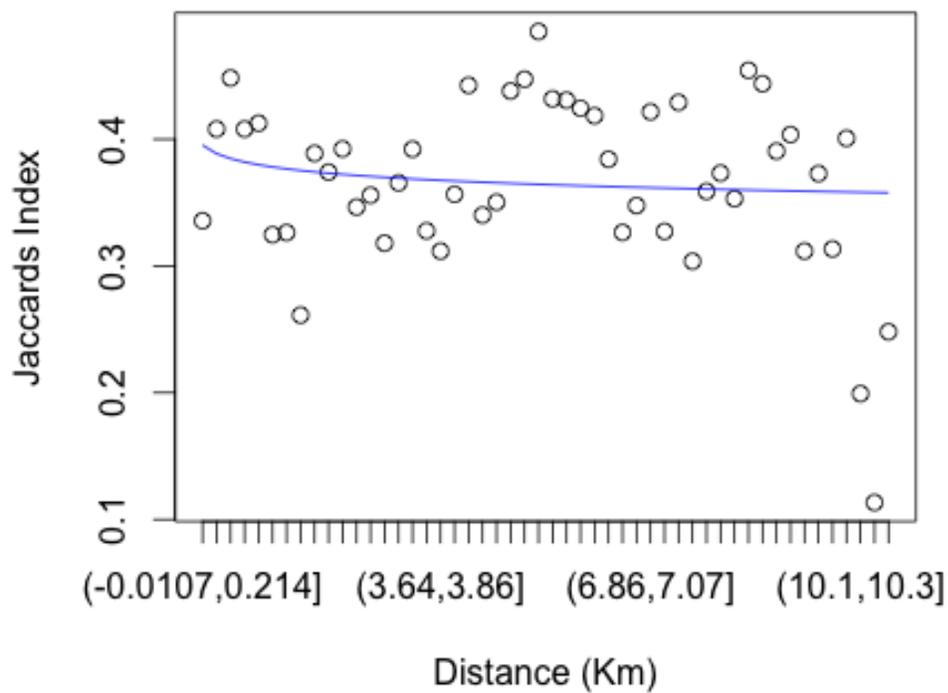


Figure 2. Logarithmic regression analysis of vesper sparrow songs. $R^2 = 0.03107$, $P = 0.0639$.

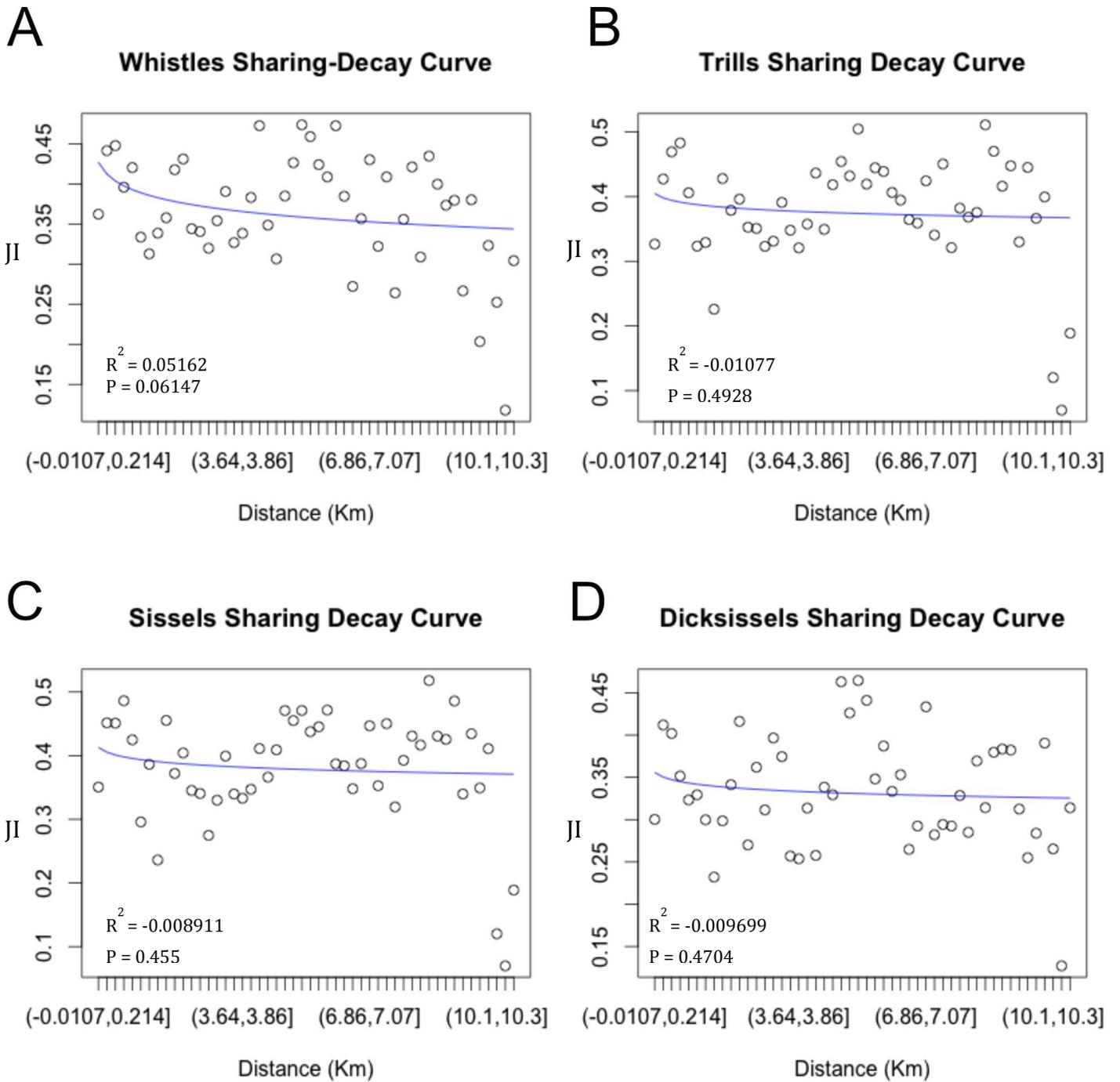


Figure 3. Logarithmic regression analysis for whistles, trills, sissels and dicksissels.

Vesper Sparrow Song Sharing Decay Curve

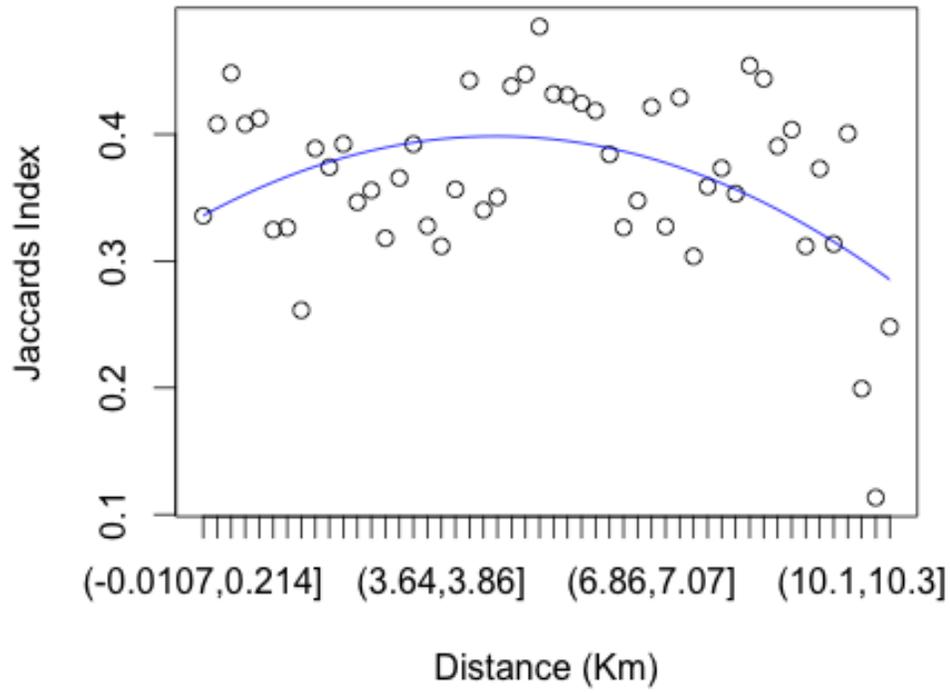


Figure 4. Polynomial regression analysis of vesper sparrow songs. $R^2 = 0.1709$, $P = 0.004587$.

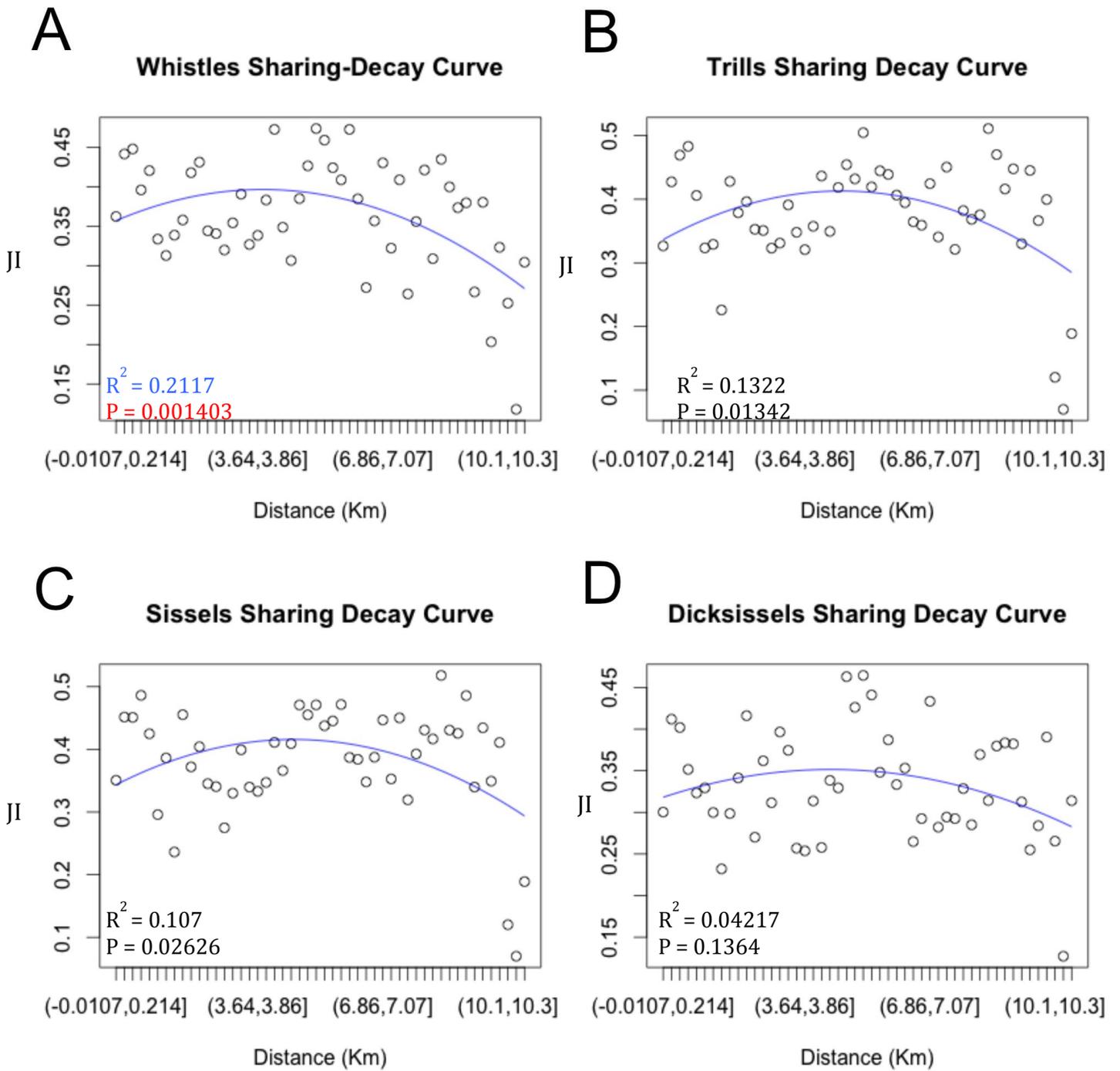


Figure 5. Polynomial regression analysis of whistles, trills, sissels and dicksissels.

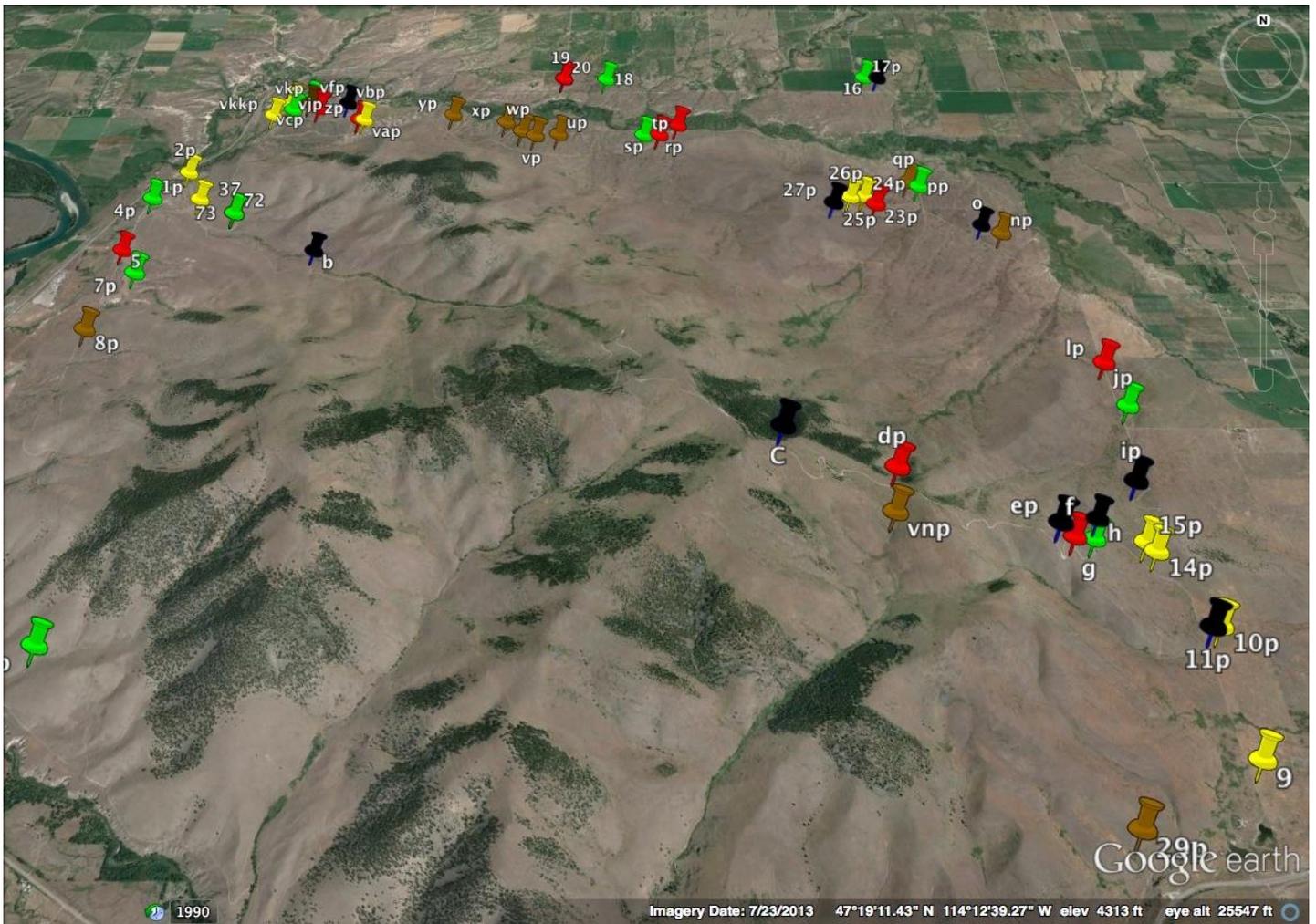


Figure 6. Map of individuals sorted into 5 different groups by descending order of Jaccard Index scores of pairwise song comparisons: “Red birds” having the highest Jaccard index scores, being more similar to one another and “Brown birds” having the lowest Jaccard Index values. R> Bl> G > Y > Br.

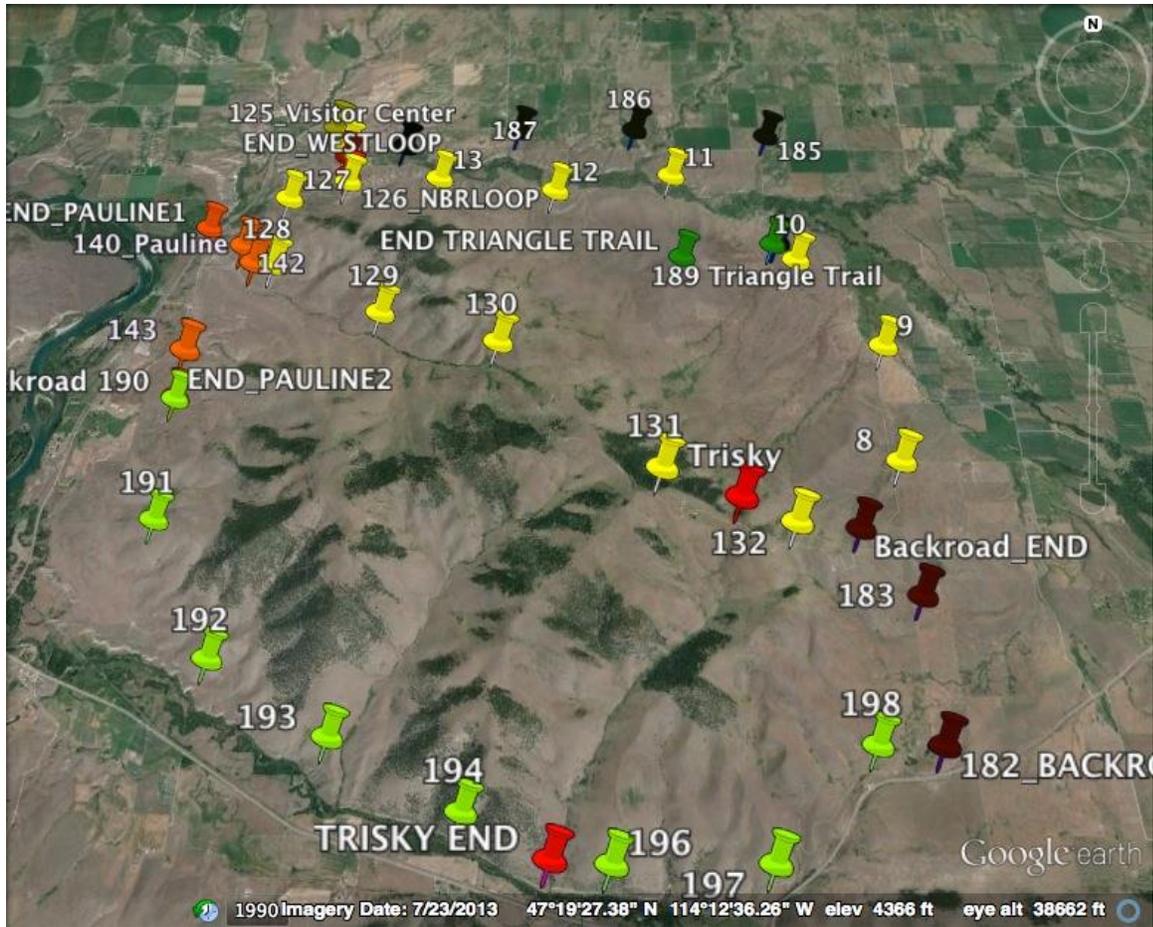


Figure 7. Map of transects where recordings were conducted. Different colours represent different roads/areas.

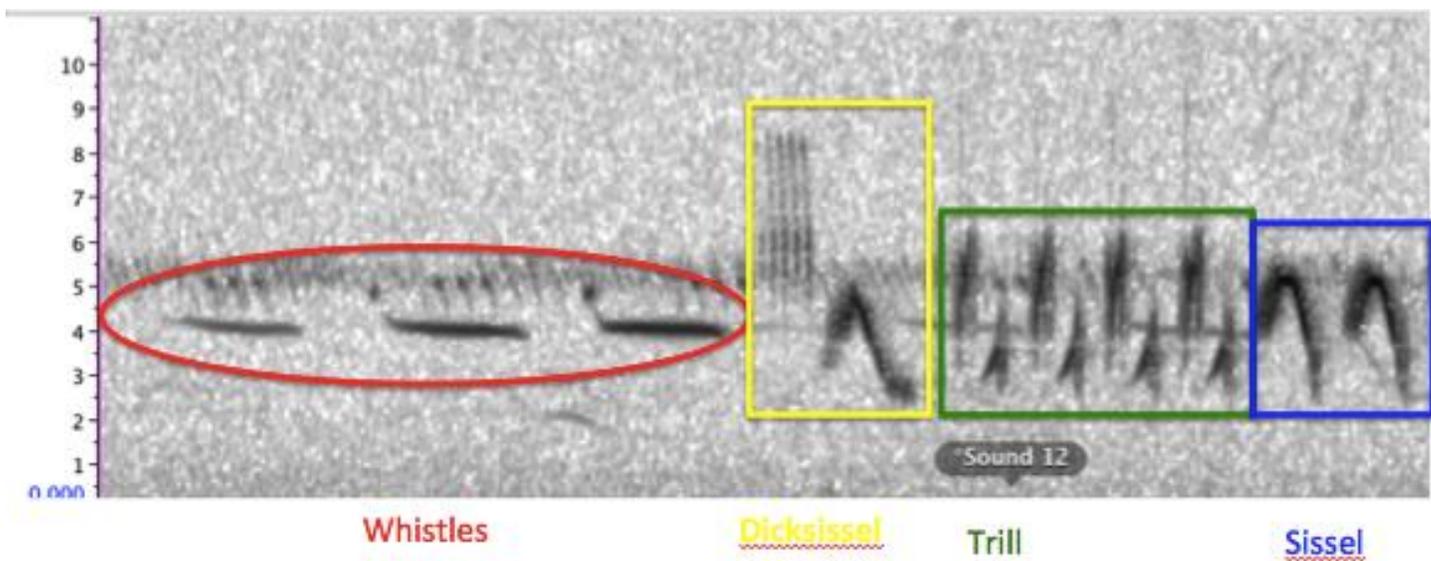


Figure 8. Example of vesper song elements and how they were categorized.

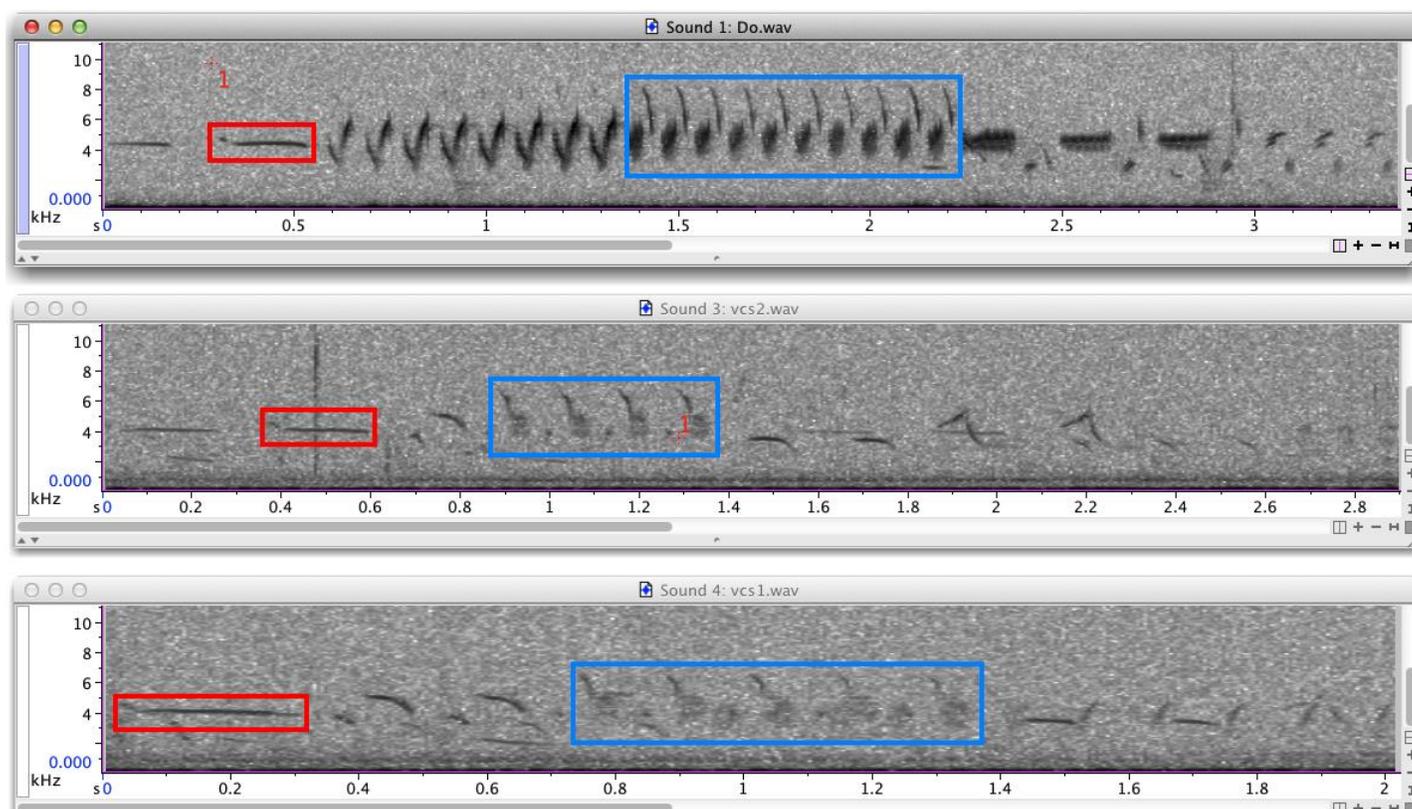


Figure 9. Sonograms of bird “D” and bird “Vc”(2 song represented by Vc). Jaccards Index Score = 0.78025. Note similarities in whistle and trill. Sonic similarities may not be clearly visualized.

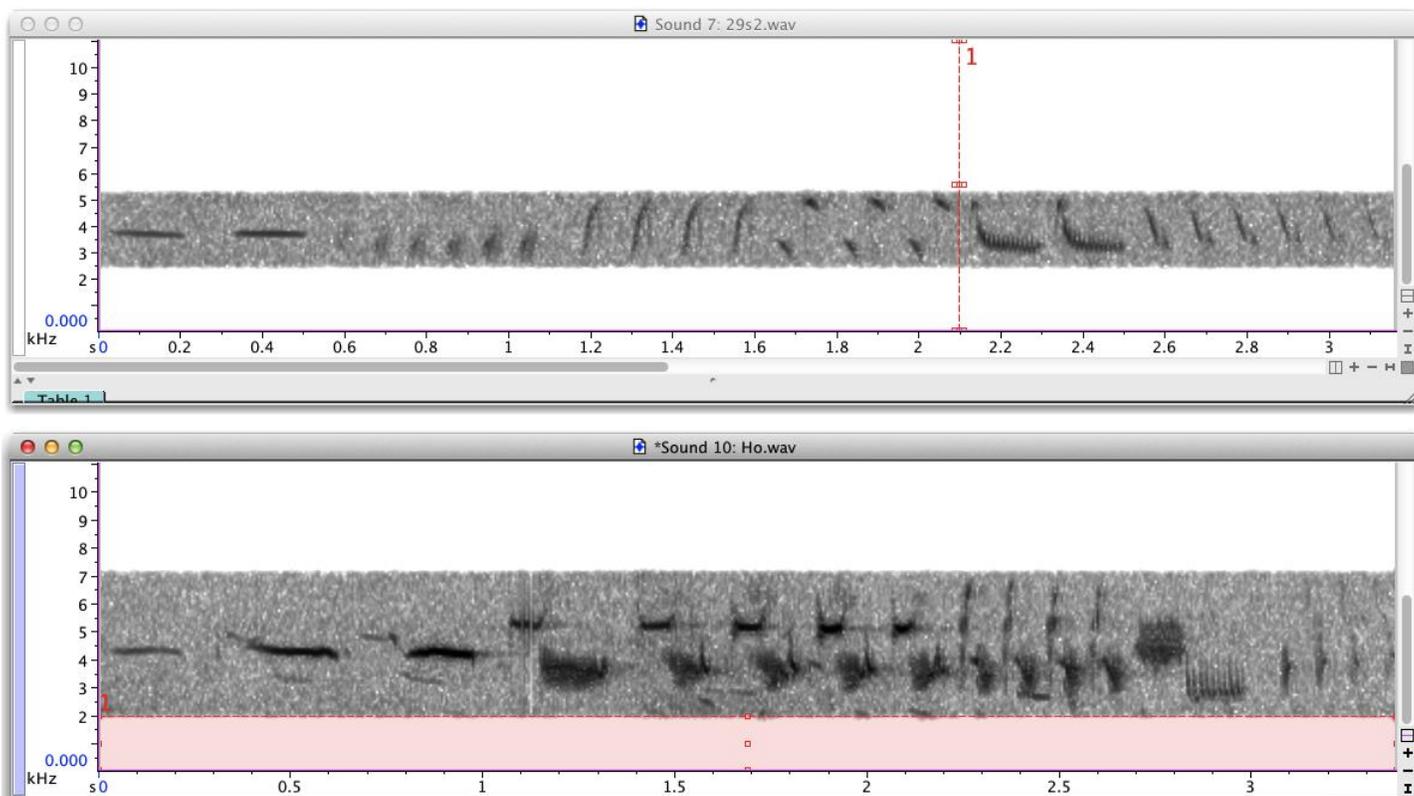


Figure 10. Sonograms of Bird 29 and Bird 10. Jaccards Index Score = $7.14E-05$.

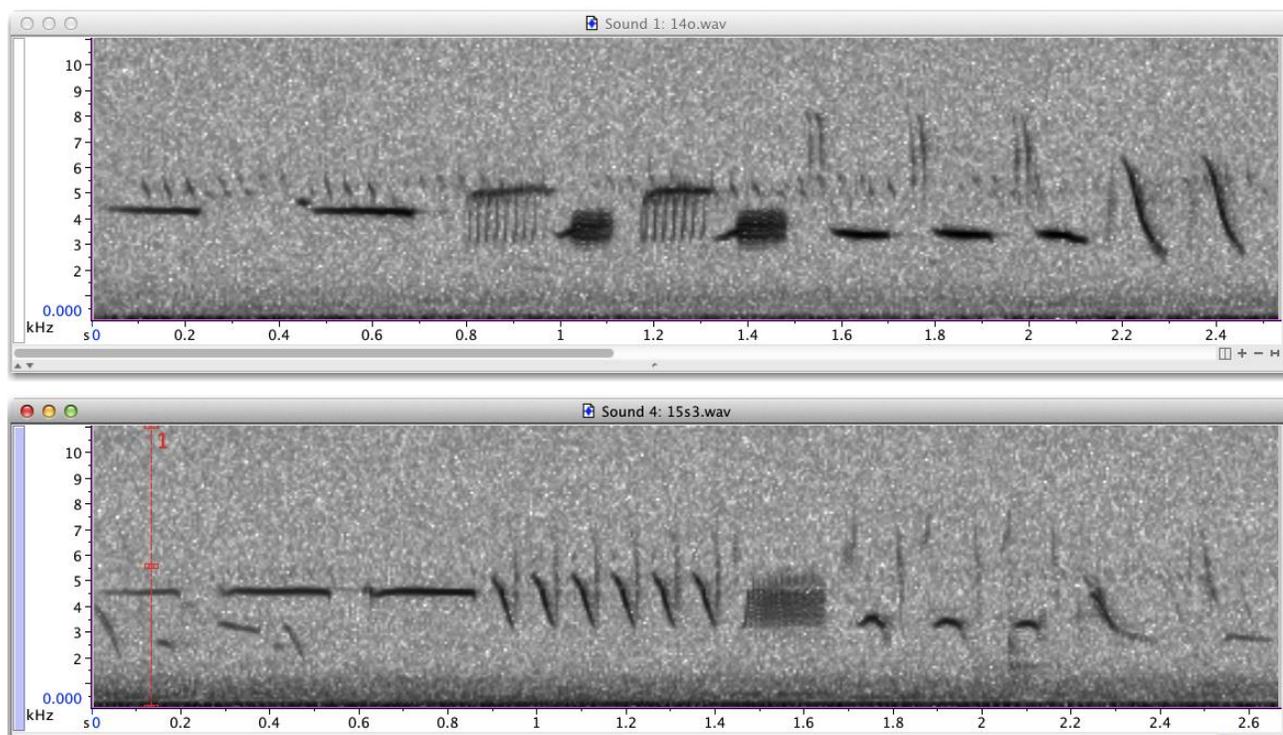


Figure 11. An example of sonograms from two vesper sparrows that were neighbors. Jaccards Index = 0.1465.