Preliminary Study in whether land management affects dialect formation in Bobolinks

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Introduction

Song dialects occur when individuals share similarity in song phrases at the group level. Most hypotheses regarding formation and maintenance of dialects attempt to explain how females select mates through preferences for local song types (Payne et al. 1981; Baker & Cunningham 1985; Rothstein & Fleischer 1987). These hypotheses predict that males attempting to breed in a particular area for the first time are under selection pressure to acquire the song type(s) most preferred by females of that area; otherwise, they will be at a disadvantage in securing a mate. Therefore, young and/or dispersing birds must learn the local songs of successfully breeding males if they are to reproduce successfully (O'Loghlen & Rothstein 2003). Substantial research on dialects and female choice as a means of sexual selection has been conducted with white-crowned sparrows (*Zonotrichia leucophrys*) regarding function and formation of song dialects. According to Lampe & Baker (1994), females seem to prefer males who sing local dialects, indicating that due to female preferences, a male who sings the local dialect is more likely to be chosen by a female over one who sings an unfamiliar song; this would, therefore, indicate that conforming to the local dialect could potentially be adaptive (Nelson 2000). MacDougall-Schackleton et al. (2002) found that mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) males singing unfamiliar songs had a lower fertilization success than those singing the local dialect; in addition, females produced disproportionately more young with males of the local dialect than those of unfamiliar dialects. There was also a correlation between song dialect and parasite load; males who sang dialects of more distant songs were more susceptible than local males to the blood-borne parasite *Haemoproteus*.

Social constraints are not the only factor influencing dialect formation, as variations in morphology and habitat structure have also been cited as mechanisms. Anderson and Conner (1985) suggested that northern cardinal (*Cardinalis cardinalis*) dialects may result from selective pressures exerted by the acoustics of the environment, based primarily on vegetative structure. The same habitat characteristics that drive song divergence may also lead to morphological divergence (Lambrechts et al. 1997). Restricted gene flow between populations can also contribute to song dialects, but more frequently depend upon learned songs because many species will adjust their song after dispersal to a new breeding area (Slabbekoorn & Smith 2002). For example, populations also form dialects when individuals copy the songs of neighbors in response to social interactions (Payne 1981). In sparkling violet-ear hummingbirds (*Colibri coruscans)* and green violet-ear hummingbirds (*C. thalassinus),* Gaunt et al. (1994) suggested that geographic variation in song results from song learning. White-crowned sparrows (*Zonotrichia leucophrys nutalli*) showed distinct song

dialects across multiple isolated populations with each population producing one or two different song types. It is even thought that dispersing males learn their songs from several other males, producing a mixture of song types from local males (Slabbekoorn et al. 2003).

Male songbirds are assumed to develop their song repertoire by imitating the songs of their territory neighbors before closure of the sensitive phase (Nelson et al. 2001). In this case, the sensitive phase persists until at least a male's second year (Nelson 2000). Therefore, newly settled birds can learn additional songs through imitating current residents during the sensitive phase, thereby assimilating the local dialect (Slabbekoorn & Smith 2002). However, after the sensitive phase, songs can no longer be memorized and incorporated into a male's repertoire (Kroodsma 1982; Marler 1997). Therefore, within these temporal constraints, it is crucial for males to develop their repertoire during the sensitive period and remain settled in the location of the learned local dialect.

I have chosen to focus on one bird species, the bobolink (*Dolichonyx oryzivorus*), whose song is culturally transmitted. However, the temporal pattern of song-learning has not been studied extensively in bobolinks. This study focuses on dialects among bobolink populations in the Champlain Valley of Vermont and New York (USA) where fields are strongly affected by hay-cutting. This major degradation of habitat quality imparts significant levels of emigration on bobolinks, thus they are a useful model to address questions of dialect formation in a human-modified environment. Additionally, there are few studies on bobolink dialects. The only documentation of bobolink dialects is that of Avery & Oring (1977). Further, of the passerines, male bobolinks have one of the most complicated songs, which can vary tremendously over space, time, and social context. Substantial variation can exist between populations and even between individuals within a given population.

Finally, there are no studies that have explored land management impacts on dialect formation in bird populations. Whether and how land management affects dialect formation has not been explored and the results of these impacts may vary based on habitat. This study can serve as a framework for future research regarding the function of dialects at the individual and group level and land management impacts on dialect formation in songbird populations. It also may provide insights into the cultural evolution of song learning and whether loss of habitat potentially promotes mutation in notes.

When fields are cut early in the breeding season (prior to mid-June), the nests fail and females will not attempt to re-nest in that field. Instead, males and females disperse and presumably re-nest on an uncut field, but neither their location nor activity following cutting has been documented. This dispersal can affect dialect formation because displaced birds who resettle on another field may be forced to adapt to the current dialect of that field or suffer reduced mating success. Although there is a high turnover rate on all fields, few adult bobolinks return to fields that were cut early in the previous year (Strong unpubl. data). Due to this high turnover, early cut fields should consist of males of different ages and different prior exposure to other dialects.

This study addresses the question of (1) whether dialects exist within and between populations of bobolinks affected by different agricultural management practices and (2) whether dialects exist between geographically distant populations. Dialects will not form on early-cut fields because of the consistent early-cutting cycles of the hayfields. However, late cut fields will show clear dialects because males will not be displaced early in the breeding season. Additionally, dialects will occur between geographically separated populations of late-cut fields. In particular, I will test the following hypotheses. First, with respect to a geographic barrier (Lake Champlain) males within a given population will sing songs more similar to songs of that population than to songs of a population separated by a geographic barrier. Second, early cut fields will have more variation in songs within a given population, while late cut fields will have more cohesive dialects. Additionally, regardless of management practices, there will be more similarity between fields in a given population.

Methods

Study species

Bobolinks are medium-sized Neotropical migratory blackbirds, who breed primarily on hayfields in North America. Their breeding range extends across the Northeast and northern Midwest into southern Canada. They exhibit sexual dimorphism, with the male being highly showy and the females being cryptic; they also tend to be polygynous, with males often pairing with 2 or 3 females. Male bobolinks are assumed to acquire their song repertoire during their first breeding season by copying the songs of other males (Avery & Oring 1977); males eventually have several varied songs within a given repertoire (Trainer & Peltz 1996). Initially, males were thought to share unique song types, each consisting of 25 to 50 notes (Avery & Oring 1977; Wittenberger 1983; Capp & Searcy 1990; Capp 1992). However, when songs were characterized as types with different functions, some of the diversity of notes were specific to particular social contexts (Trainer & Peltz 1996; Ammer & Capp 1999). Longer and more complex songs were sung during male-female contexts and shorter and simpler songs used during male-male contexts (Capp & Searcy 1991; Trainer & Peltz 1996; Ammer & Capp 1999). In this paper, I will follow the method of the Trainer & Peltz (1996), assuming that song variation rests on a continuum, rather than as discrete song types.

Study sites

The study was conducted on four private farm fields in the Champlain Valley (VT, NY, USA): Shelburne, Vermont (*n*=2), Plattsbugh (*n*=1) and Beekmantown (*n*=1), New York. The Vermont and New York field locations are $\leq$ 5.0 km from Lake Champlain. The fields are approximately 1.1 and 3.2 km apart in Vermont and New York, respectively. The Vermont and New York sites are approximately 40 km from each other. In both Vermont and New York, one field is cut early in the breeding season before or while Bobolink nests are active; the other is cut later in the breeding season after the nestlings fledge. During my research, the early cut fields, Windmill Hill of Vermont and Sonny Bubbins of

New York, were cut 28 May and 12 June 2005 respectively, and the late cut fields, Elm Marsh of Vermont and Cumberland Head of New York, were cut in mid to late August 2005.

Field observations and song sampling

Males were captured with mist nests and playbacks of conspecific song. Captured males were color banded to identify individuals, and those who were potentially not banded were identifiable by song , plumage features that make them recognizable, or by their consistent use of a particular portion of the field. All of the males were recorded during the courtship period when singing activity was most intense. I recorded un-banded males at each field only once to avoid multiple recordings of the same un-banded individual (that might be coded as a different individual). Songs were given a random number and were randomly selected from each field for analysis in order to avoid biasing results when categorizing song notes. These songs excluded spectrograms which could not be interpreted in the analysis. In addition, notes that occurred above 10 kHz were not included in the catalogue because they had little visibility on the spectrograms.

Birds were recorded from mid-May to early-July between 05:00 and 10:00 when the males are most active and when background noise was less severe (Yarbrough unpubl. data). I used a Marantz PMD61 portable solid-state digital audio recorder and a Sennheiser ME66 shotgun microphone (sample range 10 dB) to record male bobolinks. A USB 2.0 was also used to upload and download recordings (sample rate at 50 kHz and gain at 9 dB). SIGNAL 4.0 digital audio analysis program was used to produce a sound spectrogram of each song. Originally, the plan was to record at least five clear songs from each male, with a total of five males from each field. Instead, I randomly chose five songs from all of the songs recorded, regardless of the male because there was not an even total of males from each field.

Data analysis

I recorded a total of 90 songs (EM=25, WH=16, CH=18, SB=31), and spectrograms were printed of each song. Each song was catalogued and sequenced, giving each different note a unique number. Thus, notes that were found in a number of different songs all received the same number for that note whereas unique notes received unique numbers (Figure 1). Note catalogues were organized in 10 x 10 matrices for better recognition during cataloging. To analyze song similarity, I indicated the presence/absence of notes within each song and ran a hierarchical cluster analysis and a k-means cluster analysis.

Results

There were a total of 284 different notes. These notes were identified solely on visual characteristics. The mean number of notes per song was 27.72.

Hierarchical Cluster Analysis
Individual bobolinks appeared to cluster together, except for one song from SB that clustered with primarily WH songs (Figure 2). That same individual clustered with two individuals from CH, along with one other SB song. Within this cluster, some pairs within the group (but not the group as a whole), share identical songs. This may suggest previous encounters where learning could have taken place; however, where and when this could have occurred is unknown. In addition, one song is a strong outlier (WH3.05, cluster distance = 0.35), such that it does not cluster with any of the other songs, grouping most closely with one individual from WH and one individual from CH.

K-means Cluster Analysis
Due to technical difficulties, I was only able to run a 2-means cluster analysis of the entire dataset, which addressed whether there was similarity at the state level (Figure 3). The problem seemed to be that the statistical software Systat was not responding to the 90 x 284 matrix, and as a result, it repeatedly crashed. Despite that, I was able at least to run a k-means with the first 100 notes of the database, resulting in 4 clusters (Figure 3).

Songs were clustered together based on presence-absence of each note. The two charts show the percentage of songs from each field in clusters of two or four groups. With two clusters, there appears to be a distinct Vermont and a distinct New York dialect, with the exception of a few songs, all from early-cut fields that clustered with the "wrong" state. With four clusters, there appeared to be a similar pattern of state dialect, but it is less distinct, especially in cluster 1 where songs from all four fields are present. Cluster 1 is very interesting because although the majority of the songs come from Vermont, 20% of the songs are from two individuals on CH and 2% from SB. One of the CH individuals in cluster 1 did not cluster with other New York songs (cluster 3), and the other CH individual had only one song to appear in cluster 3. Additionally, with four clusters, cluster 2 and 4 represent songs from the same fields, both early-cut fields. In cluster 2, all songs are from the same individual, whereas in cluster 4, songs come from two individuals, with one also representing the SB component of cluster 1.

Discussion
The results of the cluster analysis suggest that there remain distinct state dialects, but there is still variation within and across states. Most of the dissimilarity occurs with songs from early-cut fields, but the 4-means cluster results suggest that there may be some displacement from (or movement to) late-cut fields. The variation in dialects on early-cut fields supports the hypothesis of displacement due to hay-cutting. However, there is not enough evidence based on the data shown that would strongly support hay-cutting being the sole cause of song variation. Nonetheless, with that in mind, there appears to be a difference between dialects on early-cut and late-cut fields, especially in Vermont, where this field was cut much earlier in the breeding season than in New York.

Conclusion and implications

Further study is necessary to address the presence of a geographic barrier to dialect formation and the correlation between dialect formation and reproductive success. This understanding is critical to assess whether dialect formation is a possible tool in quantifying mating success. Other questions such as the causation and function of song complexity in Bobolinks needs attention, and larger sample sizes are definitely needed. An interesting prospect to include would be additional agricultural management practices such as rotationally-grazed pasture to assess whether other management activities affect dialect formation. Statistical methods for analyzing complex signals to test group similarity/dissimilarity need to be explored. Despite the small dataset and limited time for the study, I propose that dialect formation in songbirds be given future consideration in management studies as a precursor or additional indicator for assessing the effects of human behavior on populations.
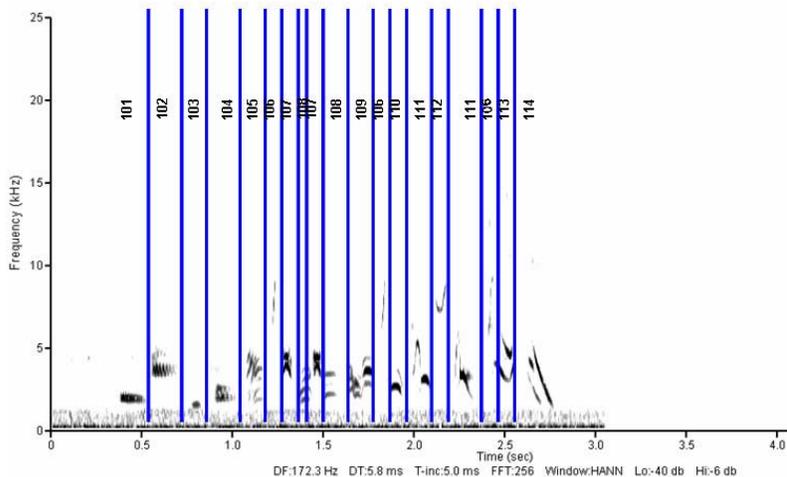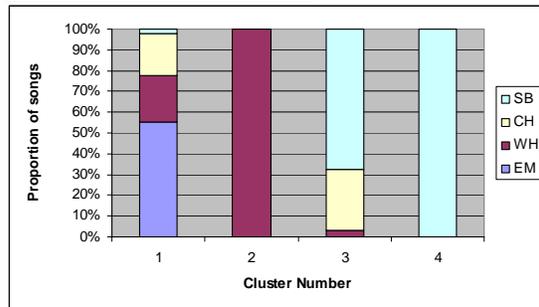

Figure 1. Spectrogram of a song catalogued where each note is identified by a given number.

Figure 2. Cluster tree result from a hierarchical cluster analysis. Distance ranges from 0.0 to 0.4, where 0.0 indicates identical songs and 0.4 indicates where all songs cluster together. Note that repertoires from individuals tend to cluster together.

First 100 notes 101-199

All 284 notes 101-286

Proportion of songs

100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%

SB
CH
WH
EM

Cluster Number
1   2   3   4

Proportion of songs

100%
90%
80%
70%
60%
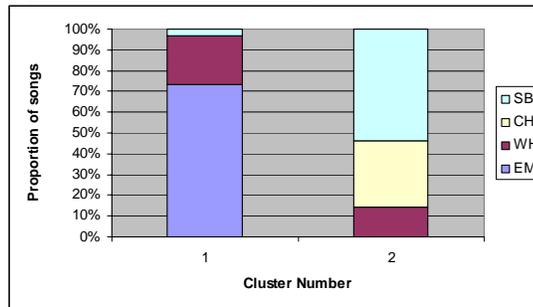50%
40%
30%
20%
10%
0%

SB
CH
WH
EM

Cluster Number
1   2

Figure 3. K-means cluster analysis showing the proportion of songs from each field in each cluster. 4-means (left) and 2-means (right).

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