



Inter-dialect dispersal is common in the Puget Sound white-crowned sparrow

Douglas A. Nelson^{a,*}, Ben M. Nickley^a, Angelika Poesel^a, H. Lisle Gibbs^a and John W. Olesik^b

^a Borror Laboratory of Bioacoustics, Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH 43210, USA

^b School of Earth Sciences, The Ohio State University, Columbus, OH 43210, USA

*Corresponding author's e-mail address: nelson.228@osu.edu

Received 1 April 2017; initial decision 24 May 2017; revised 14 June 2017; accepted 21 June 2017; published online 12 July 2017

Abstract

Dispersal in birds can have an important influence on the genetic structure of populations by affecting gene flow. In birds that learn their songs, dispersal can affect the ability of male birds to share songs in song dialects and may influence mate attraction. We used Inductively Coupled Plasma Mass Spectrometry (ICP-MS) trace element analysis on the body feathers of birds to assess dispersal among four song dialects. We found that (1) most males had a feather element profile typical of only one dialect location; (2) males singing non-local ('foreign') dialects in a focal population often learned their foreign songs outside the dialect; and (3) females often dispersed among dialects. We estimated 5% dispersal per year by yearling males between the site of moulting and breeding. Our estimate is consistent with genetic estimates of widespread gene flow between dialects in this subspecies of the white-crowned sparrow.

Keywords

dispersal, trace elements, song dialects, song learning, *Zonotrichia leucophrys*.

1. Introduction

Dispersal of animals can have important effects on behaviours that influence the dynamics and genetic structure of populations. One such behavioural process in song birds is song learning. As far as is currently known, young males of most song bird species learn their songs from adult 'tutors', although the timing of and the form of his learning varies considerably among species

(Catchpole & Slater, 2008). In some species, males learn their song(s) in the first few months of life, the same time frame that they leave their natal territories and prospect for a future breeding territory (Beecher et al., 1994; Nelson & Poesel, 2014). In other species learning new songs occurs later in life during the bird's first breeding season (O'Loughlen & Rothstein, 1993; Briskie, 1999). When dispersal from the site of learning is limited, males with shared song types cluster together in small song neighbourhoods or larger vocal dialects. In several species males appear to benefit from breeding in the same area where they learned their song(s) early in life, perhaps because they have prior experience with the area and/or their shared songs allow them to communicate more effectively with conspecifics (Payne et al., 1988; Beecher et al., 2000; Poesel et al., 2012).

Although song dialects can be quite homogeneous, it is commonly observed that some males within a local dialect sing songs typical of a foreign dialect — redwing, *Turdus iliacus* (Bjerke & Bjerke, 1981); corn bunting, *Emberiza calandra* (McGregor, 1980; Hegelbach, 1986; Glaubrecht, 1991); ortolan bunting, *Emberiza hortulana* (Conrads, 1976); white-crowned sparrow, *Zonotrichia leucophrys* (Cunningham et al., 1987); savannah sparrow, *Passerculus sandwichensis* (Bradley, 1994). The existence of such foreign singers provides evidence that males do disperse between dialects. However, it is unclear in cases where multiple 'foreign' singers exist in a population whether each bird represents an independent dispersal event, or instead is a local male that learned a foreign dialect from a single immigrant. Ideally, banding data of individuals of known origin can help answer this question, but such data are difficult to obtain because recapture rates of fledgling songbirds are low (Webster et al., 2002; Nathan et al., 2003). Few studies have directly estimated dispersal of banded birds among dialects. In Nuttall's white-crowned sparrow, *Zonotrichia leucophrys nuttalli*, Baker (1978) found that fewer juveniles crossed a dialect boundary than expected by a null model, while brown-headed cowbirds, *Molothrus ater* (Anderson et al., 2005), and yellow-rumped caciques, *Cacicus cela*, moved freely among dialects (Trainer, 1989).

Here we apply a different technique to estimate dispersal among dialects: comparison of the trace element composition of feathers. This method has been used to track movements in several species of birds (Kelsall & Burton, 1979; Szép et al., 2003; Donovan et al., 2006; Gómez-Díaz & González-Solís, 2007; Norris et al., 2007; Óvári et al., 2016). Trace elements differ

from stable isotopes in that they do not vary in a predictable pattern across the landscape, but depend on local features (Adout et al., 2007). We have previously shown in a pilot study (Poesel et al., 2008) that the elemental composition of feathers grown during summer body moult in Puget Sound white-crowned sparrow males (*Z. l. pugetensis*) differs among four locations in different vocal dialects along the Pacific northwest coast of North America. In the case of our study species, we assume that trace elements vary among river basins that have differing bedrock and sediments along the Pacific coast (Poesel et al., 2008). We apply this technique here to a larger sample of males, as well as females, and conduct a detailed analysis of the song repertoires of possible immigrant males.

The Puget Sound white-crowned sparrow breeds in coastal dunes and forest openings, forming a linear series of song dialects along the coast (Baptista, 1977; Nelson et al., 2004). The dialects are defined by the terminal trill of the song (Figure 1) and at least 85% of males within a local population sing the same dialect (Baptista, 1977; Soha et al., 2004). The majority of adult white-crowned sparrow males sing a single song type. The ability to imitate a tutor appears to be restricted to the male's hatching-year summer, as we have never observed a male learn a new song after arriving on his breeding territory as a yearling (Nelson, 1999, 2000; Nelson & Poesel, 2009). Nevertheless, young males retain some flexibility to modify their song repertoire after dispersing to their first breeding territory. About half of yearlings arriving at the beginning of the breeding season sing two or more song types, i.e., overproduce song, before they discard the extra type(s) and retain the one song type resembling the type sung by most of their territorial neighbours (Nelson, 2000). The fact that some males sing two or more different dialects in their overproduced repertoire (Nelson, 2000; Nelson & Poesel, 2009), raises the question of where males learned their song repertoire.

Our study has three goals: first, we test the hypothesis proposed in Poesel et al. (2008) that the feather element 'signature' of a yearling male that sings two or more dialects represents the mixture of elements acquired in all localities during the male's sensitive phase for song learning. This hypothesis makes two predictions: males that overproduce dialects should be difficult to classify accurately to one location based on their feather composition because the feathers would contain a mixture of elements from two or more locations, and a measure of the male's foreign dialect song composition should correlate with an estimate of how likely he was in a foreign dialect

the previous summer. Second, we estimate how often foreign dialects are learned outside the local dialect as opposed to learned from the rare foreign-singer within a local dialect. Third, we estimate inter-dialect movements of breeding females in addition to those of males. In birds, natal and breeding dispersal occurs more often and over longer distances by females than by males (Greenwood & Harvey, 1982; Clarke et al., 1997; Mabry et al., 2013), and we test whether this technique detects the same sex difference. Widespread dispersal among dialects by either males or females could be one explanation for the common finding that different song dialects in birds do not differ genetically (Poesel et al., in press).

2. Materials and methods

2.1. Field methods

We collected feathers and recorded songs from *Zonotrichia leucophrys pugetensis* in four different song dialects along a 388 km stretch of the Pacific northwest coast (Figure 1). The sites sampled from south to north were Cape Blanco State Park (42.840°N, 124.542°W), Bullard's Beach State Park (43.137°N, 124.417°W; 40 km north of Cape Blanco), Oregon Dunes National Recreation Area, 12 km southwest of Reedsport (43.647°N, 124.208°W; 95 km north of Cape Blanco), and Cape Disappointment State Park (46.278°N, 124.074°W; 388 km north of Cape Blanco; note that the last site was previously named Fort Canby State Park). With the exception of Cape Blanco, each sample location was in coastal dunes at a river mouth. Males at Cape Blanco bred in parkland along the Sixes River or in a forest opening on a plateau 60 m above the river.

At our two main study sites we monitored the arrival of males from migration each year and recorded their song repertoires at least weekly between late March and late May. We worked at Bullard's Beach between 2004 and 2008 (Nelson & Poesel, 2009), and at Cape Disappointment between 1997 and 1999 (Nelson, 2000). Most males in these two populations were colour-banded, so we are confident that the sampled males at these locations were breeding for the first time in those study areas and were probably yearlings, based on partial brown crown colour and/or their short wings (Nelson & Poesel, 2009). In the mountain white-crowned sparrow, *Z. l. oriantha*, both male and female yearlings have shorter wings than their same-sex adult counterparts (Morton, 2002). Males at Reedsport and Cape Blanco were a mixture

of yearling and older (hereafter ‘adult’) birds. Six females were yearlings based on crown colour and an additional seven black-and-white-crowned females were probable yearlings based on their short (<66 mm) wing length. Hatching-year birds of this species have a partial pre-basic moult in which the body, but not flight feathers, are moulted, while after-hatch-year birds have a complete moult (Grinnell, 1928; Pyle et al., 1987; Morton, 2002). To our knowledge, nothing is reported of age differences in the timing of this moult. In captivity, males begin moult about two weeks before females (Mewaldt & King, 1978). The pre-alternate moult in all age classes is confined to the head and neck region in which brown-crowned yearling birds acquire the black-and-white striped crown of adults (Grinnell, 1928).

We caught males during the breeding season by broadcasting white-crowned sparrow song from a loudspeaker in front of a mist net. Breeding females were captured at Bullard’s Beach in traps or mist nets. We collected two to three flank feathers and stored them in sealed and labelled plastic bags until we analysed them in the laboratory in Columbus, Ohio. We sampled flank feathers because, based on examination of 80 museum specimens, they are grown during the partial pre-basic moult the previous summer and not during the partial pre-alternate moult (Poesel et al., 2008), and this allowed us to estimate where the bird was in mid to late summer, during or after the sensitive phase for song learning in males sampled as yearlings. We banded all birds with a numbered USFWS band. We recorded songs with a Sennheiser MKH70 ‘shotgun’ microphone and Rycote windscreen and a Sony TCD-D10 Pro II DAT recorder or a Marantz PMD670 solid-state recorder sampling at 48 kHz, 16-bit amplitude resolution.

We analysed four samples of birds: the first was a model sample consisting of feathers and songs of local dialect singers sampled in the four different locations, the second sample consisted of nestlings from Bullard’s Beach, the third included yearling males at Bullard’s Beach that sang one or more song types typical of a foreign dialect, and the fourth included breeding females at Bullard’s Beach. The model sample was used to build two discriminant functions models to estimate whether (a) feather elements and (b) song structure differed among the four sample localities. The second sample was used to validate the model sample using birds (nestlings) of known origin. The feather element and song structure discriminant models were used to classify the moult locality and song dialects of the males in the third sample, while

the feather element model was used to identify the previous moult locality of females.

At Bullard's Beach and Cape Disappointment some males in the model sample overproduced song types upon their arrival, but all types were typical of the respective local dialects. We collected feathers from 25 breeding adult males at Bullard's Beach between 2004 and 2008, 14 at Cape Blanco in 2005, 11 at Reedsport in 2006, and 21 at Cape Disappointment in 1998 ($N = 71$ males in the feather model sample). For the song model sample ($N = 92$ males), we recorded the songs of most males that were in the feather model sample: all 25 males at Bullard's Beach, 19 of the 21 males at Cape Disappointment, and all 11 males at Reedsport. We added songs from 14 males at Reedsport also recorded in 2006 to increase sample size to 25. We did not record songs when feathers were sampled at Cape Blanco in 2005 and used songs from 22 males recorded at Cape Blanco in 2008 instead. Songs remained very similar at Cape Blanco between 1999 and 2013 so we assume it is valid to use songs recorded in 2008 to correlate with feathers collected in 2005 (Nelson et al., 2004; Nelson, 2017). The second sample of feathers consisted of feathers from 23 nestlings at Bullard's Beach (13 males, 10 females; sexed by molecular markers (Poesel et al., 2012)). Three of the male nestlings were later recaptured as breeders at Bullard's Beach and are included both in the samples of nestlings and adults. The third sample consisted of the feathers and song repertoires of 21 territorial yearling males at Bullard's Beach between 2004 and 2008 that sang some non-local song in their overproduced repertoire (hereafter 'foreign-singers'). Twenty-six of the males in the model sample and six of 21 foreign-singers were described in Poesel et al. (2008). The fourth sample contained feathers only (females rarely sing in this species) from 35 breeding females captured near their nests at Bullard's Beach from 2005 to 2007.

2.2. Trace element analysis

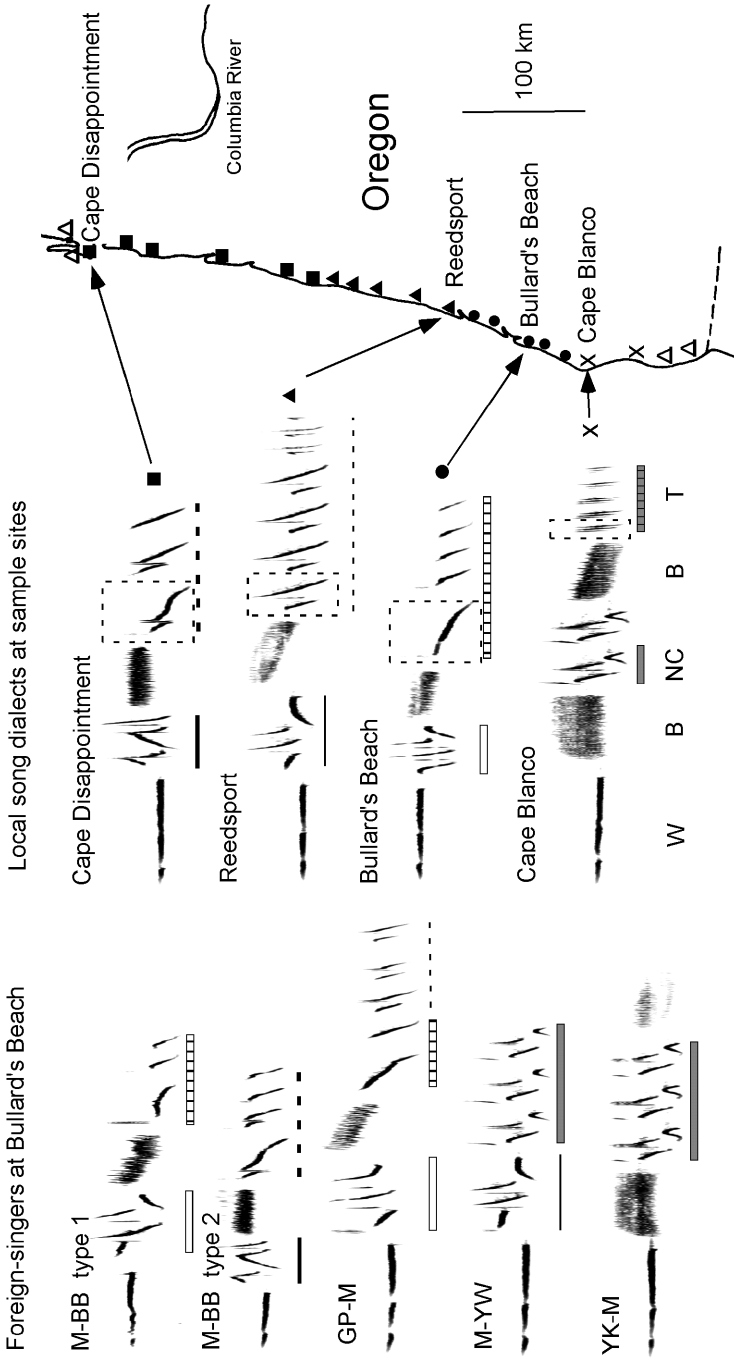
To measure trace elements in feather samples we followed Poesel et al. (2008), and used an Inductively Coupled Plasma Mass Spectrometer (ICP-MS) for a semi-quantitative analysis. We performed all analyses at the Trace Element Research Laboratory at The Ohio State University, Columbus, OH, USA. Specifically, feather samples were rinsed with distilled water, oven-dried at 37.8°C, and 2 mg of feathers from each individual weighed out to the nearest 0.1 mg in a 15-ml or 50-ml polyethylene test tube. One ml of

concentrated, purified nitric acid was added and tubes were immersed in boiling water for six minutes or until the feathers had entirely dissolved. Once cooled, we added ultra-pure deionized water to the 10-ml mark.

We used a PerkinElmer Sciex ELAN 6000 ICP-MS to analyse the prepared samples and normalized intensities for isotopic abundance as described in Poesel et al. (2008). Of the 70 elements analysed, 34 were measured reliably and were present in some feather samples: Al, As, Ca, Cd, Ce, Co, Cr, Cu, Fe, Ga, I, K, La, Mg, Mn, Mo, Nb, Nd, Ni, P, Rb, Th, Sb, Sc, Se, Sn, Sr, Tb, Ti, U, Y, V, Zn and Zr.

2.3. *Song analysis*

White-crowned sparrow songs consist of four different phrase types: whistle, buzz, note complex (also termed complex syllables; Baptista, 1977) and trill (Figure 1). Geographic variation in song of Puget Sound white-crowned sparrows is most pronounced in the note complex and terminal trill phrases (Baptista, 1977; Nelson, 2017). Note complex and trill phrases consist of one or more notes — continuous tracings on a sound spectrogram, separated from other tracings by at least 3 ms. Accordingly, we measured 13 acoustic variables on the note complex and five variables on the first syllable in the trill as described in detail elsewhere (Nelson & Poesel, 2007). For each of the first three notes in the note complex and the first note in the trill we measured: frequency at note onset, frequency at note ending, note duration, total duration of the note complex or trill syllable, and the quiet interval to the next note (the latter measure for only the first two notes). In addition, for the trill we counted the number of elements in the note: regions within a note with a constant rate and direction of frequency modulation. Measurements were made using a screen cursor and a program run in Signal 5 (Engineering Design, 2009) on spectrograms (sampling frequency 25 000 Hz, FFT length 256 points; time resolution 10 ms; frequency resolution 98 Hz). Note onset and offset were measured at the point where amplitude was -21 dB relative to peak amplitude in the phrase. We only measured the first note in the trill in this study because it is diagnostic of each sample site; subsequent notes are either repetitions of the first (Cape Blanco) or differ from the first but are also geographically unique and would likely add no new discriminating information (Figure 1).



2.4. Statistical analyses

2.4.1. Trace element analysis

We performed forward stepwise linear discriminant function analysis (LDFA) on untransformed concentration values of 34 elements in the 71 males in the model feather sample to investigate whether trace elements differed among the four locations. We built models to minimize Wilk's λ ; variables with $F \leq 3.84$ entered the model and variables with $F \geq 2.71$ were removed. Using the variables selected in the model sample, we then classified feathers in the three other samples from Bullard's Beach to one of the four source populations: (1) 23 chicks, (2) 21 foreign-singers and (3) 35 female breeders. In classifying cases to location, we assumed prior probabilities of group membership to be equal, a pooled within-groups covariance matrix, and used the leave-one-out method on the model sample to ensure that classified cases were independent of those used to build the model. We compared the percentage of cases correctly classified to the proportional chance criterion, which takes into account differences in sample size across groups (Morrison, 1969). Analyses were performed in SPSS 22.0.

2.4.2. Song analysis

We used acoustic measurements on recordings of the 92 songs in the song model sample to build discriminant functions models, one for note complexes and one for trills, to separate the four dialects and to classify the note complexes and trills of males in the model sample (by the leave-one-out method). The models were then used to classify the dialect origin of phrases in the songs of the 21 foreign-singers at Bullard's Beach. Of these 21 males,

Figure 1. The map of the Oregon coast on the right shows the distribution of the four song dialects based on recording localities in Nelson (2017) along with the four sample localities in the present study. Open triangles denote dialects north and south of the four studied here. Puget Sound white-crowned sparrow song types typical of the local dialect at each of four sampling locations are in the middle column, and examples of five song types from foreign-singers at Bullard's Beach state park are on the left (males identified by color-band codes). Four different phrase types, whistle (W), note complex (NC), buzz (B) and trill (T) are identified at the bottom of the middle column. Note complexes are identified by solid underlining, entire trills by dashed lines or cross-hatching. Note complexes and trills of the foreign singers are identified to their dialect source, as classified by discriminant functions analyses and indicated by the same pattern of underlining. Dashed boxes surround the first syllable in each trill that was measured in the acoustic analysis (see text). The five song types by the foreign-singers are described in the text.

three sang ‘hybrid’ note complexes and three sang hybrid trills composed of two different note complex or trill types (Figure 1). For these six males, we measured both note complexes or trills in each song type and classified them as described below. The final sample from these 21 males included 44 note complexes and 35 trills (nine songs lacked trills).

We built linear discriminant functions models using the same assumptions as described for the feather model sample. We then calculated the percentage of phrases that was of foreign origin (defined as any non-Bullard’s Beach dialect) in each of the 21 foreign-singers’ repertoires.

3. Results

3.1. Model sample feathers

A stepwise LDFA using three functions retained nine of the 34 measured trace elements (Table 1) and correctly assigned 76% of the 71 individuals in the model sample to their sample location (Figure 2, Table 2) as compared to 27.3% expected by chance. The first two functions explained 83% of the total variance among locations and correlated with Magnesium, Strontium, Neodymium, Zinc, Iodine and Rubidium (Table 1). Thus, different song dialect locations differ in trace element composition.

3.1.1. Assignment of known individuals: nestlings at Bullard’s Beach

The LDFA model using feather elements classified all 23 chicks sampled from nests at Bullard’s Beach to Bullard’s Beach (Table 3). All three of the male nestlings that returned to breed were classified to Bullard’s Beach using feathers sampled in their first or second breeding season.

3.2. Model sample songs

Separate LDFA models based on the acoustic structure of note complexes (Table 4 and Figure 3a) and trills (Table 5 and Figure 3b) revealed that both phrases differed significantly among the four dialects in the model sample. Trills were slightly more diagnostic of geographic identity as 92% of 92 cases were correctly assigned to dialect, versus 80% of 92 note complexes (25.3% expected by chance in both models). Most classification errors of note complexes (17) involved confusing Bullard’s Beach with Reedsport, the next dialect to the north (Table 6).

Table 1.

Stepwise linear discriminant functions analysis of the element composition of feathers in Puget Sound white-crowned sparrow males.

| | Function | | |
|------------------|----------|--------|--------|
| | 1 | 2 | 3 |
| Eigenvalue | 1.97 | 1.27 | 0.67 |
| % variance | 50 | 32 | 17 |
| Wilks' λ | 0.089 | 0.264 | 0.599 |
| Mg | 0.30 | −0.09 | −0.20 |
| Zn | 0.09 | 0.58 | 0.27 |
| I | −0.07 | 0.44 | 0.12 |
| Rb | 0.15 | 0.42 | −0.11 |
| Nd | −0.21 | 0.05 | −0.49 |
| Sr | 0.27 | 0.25 | −0.33 |
| Fe | 0.05 | 0.08 | 0.26 |
| Ce | 0.191 | −0.121 | −0.189 |
| Sn | −0.172 | 0.012 | 0.170 |

Nine of 34 elements measured were retained in the final model. $N = 71$ males in the model sample. All three functions are significant ($p < 0.001$). Values listed for each element are the pooled within-groups correlation coefficient between the element and each function.

3.2.1. Assignment of unknown individuals: foreign-singers at Bullard's Beach

The 21 foreign-singers at Bullard's Beach sang a total of 40 song types in their repertoires, with a median of two song types per male (1 song type: 8 males; 2 types: 7 males; 3 types: 6 males). The LDFAs using the model sample of songs from the four dialects classified each of the note complexes ($N = 44$) and trills ($N = 35$) in these song types to the most likely dialect of origin (Table 6). Of the 29 note complexes in this sample classified to Bullard's Beach or Reedsport (the locations with similar note complexes: Table 3), only one was a borderline decision (posterior probability = 0.46 Bullard's Beach versus 0.54 Reedsport). We accepted the LDFA dialect classifications in this and all other cases. Both the note complex and trill in 10 song types were classified to Bullard's Beach (e.g., male M-BB type 1 in Figure 1). In 16 song types one phrase was classified as Bullard's Beach and the other phrase to a different dialect, forming a hybrid song type (e.g., GP-M in Figure 1). In 14 song types all phrases were classified to dialects other than Bullard's Beach: in 11 of these all phrases came from the same dialect (M-BB type 2 in Figure 1), in three songs two phrases were classified to

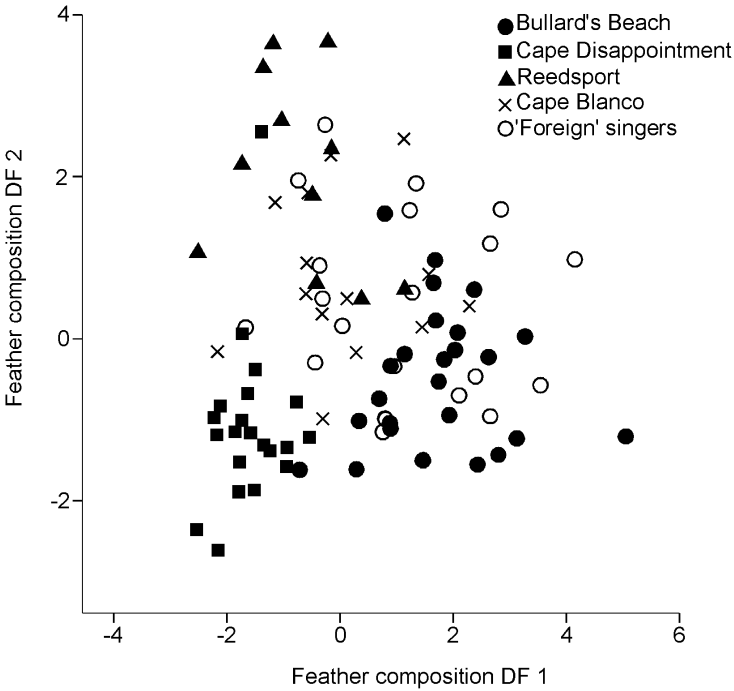


Figure 2. Scatterplot of the first two discriminant functions based on nine trace elements (Table 1) in flank feathers of Puget Sound white-crowned sparrow males. The different symbols correspond to the four sample locations as in Figure 1; open circles correspond to the 21 males at Bullard’s Beach with one or more foreign song phrases in their repertoires.

different foreign dialects (M-YW in Figure 1). All foreign-singers that sang songs with Cape Blanco note complexes omitted the trill (YK-M in Figure 1), as was also common in males at Cape Blanco. Based on the classification, five of the 21 foreign-singers sang only foreign songs in their repertoire, the remaining 16 sang phrases from both foreign dialects and Bullard’s Beach.

3.3. Goal 1: feather element signature of foreign-singers

Based on the element composition of their feathers, 11 of 21 foreign-singers at Bullard’s Beach were classified to a foreign location (Table 3). As our first goal, we hypothesized that if males visited several locations during the previous moult, their feather composition would reflect a ‘blending’ of the feather signatures at two or more locations. This hypothesis predicts that foreign-singers that learned two or more dialects would be difficult to classify with high certainty, but this prediction was not met. The distribution of posterior

Table 2.

Leave-one-out classifications based on trace elements in body feathers in four samples of white-crowned sparrows.

| Actual location | Predicted location | | | |
|---------------------|--------------------|-------------|-----------|---------------------|
| | Bullard's Beach | Cape Blanco | Reedsport | Cape Disappointment |
| Bullard's Beach | 20 (80%) | 1 | 2 | 2 |
| Cape Blanco | 3 | 8 (57%) | 1 | 2 |
| Reedsport | 1 | 2 | 7 (64%) | 1 |
| Cape Disappointment | 0 | 2 | 0 | 19 (90%) |

Percentage correct classification is shown on the diagonal.

probabilities of classification to Bullard's Beach for the 16 foreign-singers that learned two dialects did not differ significantly from the 25 males from Bullard's Beach in the model sample (Kolomogorov–Smirnov $Z = 0.937$; $N = 25, 16$; exact $p = 0.27$; Figure 4a). The distribution for the foreign-singers is somewhat bimodal, but there are few intermediate cases in Figure 2 or Figure 4a, as would be expected if feathers incorporated elements from two or more locations. Most foreign-singers were clearly assigned to one location, either a foreign one or Bullard's Beach. The maximum posterior probability of classification to any location did not differ between the model sample and these 16 foreign-singers at Bullard's Beach (Mann–Whitney

Table 3.

Classification to location based on the element composition of feathers in four samples of white-crowned sparrows.

| | Predicted location | | | | Total N |
|-----------------------|--------------------|-------------|-----------|---------------------|-----------|
| | Bullard's Beach | Cape Blanco | Reedsport | Cape Disappointment | |
| Model (leave-one-out) | 20 | 1 | 2 | 2 | 25 |
| Nestlings | 23 | 0 | 0 | 0 | 23 |
| Foreign-singers | 10 | 6 | 3 | 2 | 21 |
| Female adults | 13 | 2 | 5 | 2 | 22 |
| Female yearlings | 9 | 2 | 2 | 0 | 13 |

The first row consists of the model sample of yearling males from Bullard's Beach (the first row in Table 2) for comparison to the three other samples, all of birds sampled at Bullard's Beach, classified to location by the model sample. Female age classifications defined in the text.

Table 4.

Stepwise discriminant functions analysis of note complex acoustic structure in songs in the model sample from four locations ($N = 92$).

| | Function | | |
|----------------------|----------|-------|-------|
| | 1 | 2 | 3 |
| Eigenvalue | 21.08 | 2.93 | 0.3 |
| % variance | 87 | 12 | 1 |
| Wilks λ | 0.009 | 0.196 | 0.769 |
| Note 1 interval | 0.44 | -0.20 | 0.18 |
| Note 3 duration | 0.05 | 0.51 | -0.19 |
| Note 1 duration | 0.33 | 0.34 | 0.18 |
| Note 2 end frequency | 0.19 | 0.40 | -0.61 |
| Note 3 end frequency | 0.20 | -0.42 | -0.59 |
| Note 2 interval | -0.001 | -0.21 | 0.51 |
| Note 1 end frequency | -0.17 | -0.02 | -0.37 |

Seven of 13 measured variables were retained in the best model. All three functions are significant ($p < 0.001$). Values listed for each measurement are the pooled within-groups correlation coefficient between the variable and each function.

$U = 154$; $N = 25, 16$; exact $p = 0.227$; Figure 4b). Only four foreign-singers were borderline classification cases with a maximum assignment probability of 0.58 or less. That is, the multi-dialect foreign-singers could be classified to one of the four locations with as much certainty as model males.

To address the second prediction derived from the hypothesis that foreign-singers would have a blended feather element profile, we calculated the percentage of foreign phrases within the entire repertoires of all 21 foreign-singers. Six males had song repertoires in which all song type(s) were composed entirely of foreign phrases, all of these males were classified to a foreign location based on their feather composition. In four of these males all phrases in their song matched the location based on their feather signature, in one male 75% of his phrases matched his feather location classification, and in the sixth male the song and feather classifications disagreed. The remaining 15 males had 17 to 75% of their phrases across all their song types classified as foreign in origin. Ten of these 15 males were classified to Bullard's Beach based on feathers, the other five were classified to a foreign location. The dialect classifications based on feathers and song agreed for all but two of the 15 males. The percentage of foreign phrases within the repertoires of all 21 foreign-singers was significantly correlated with the posterior

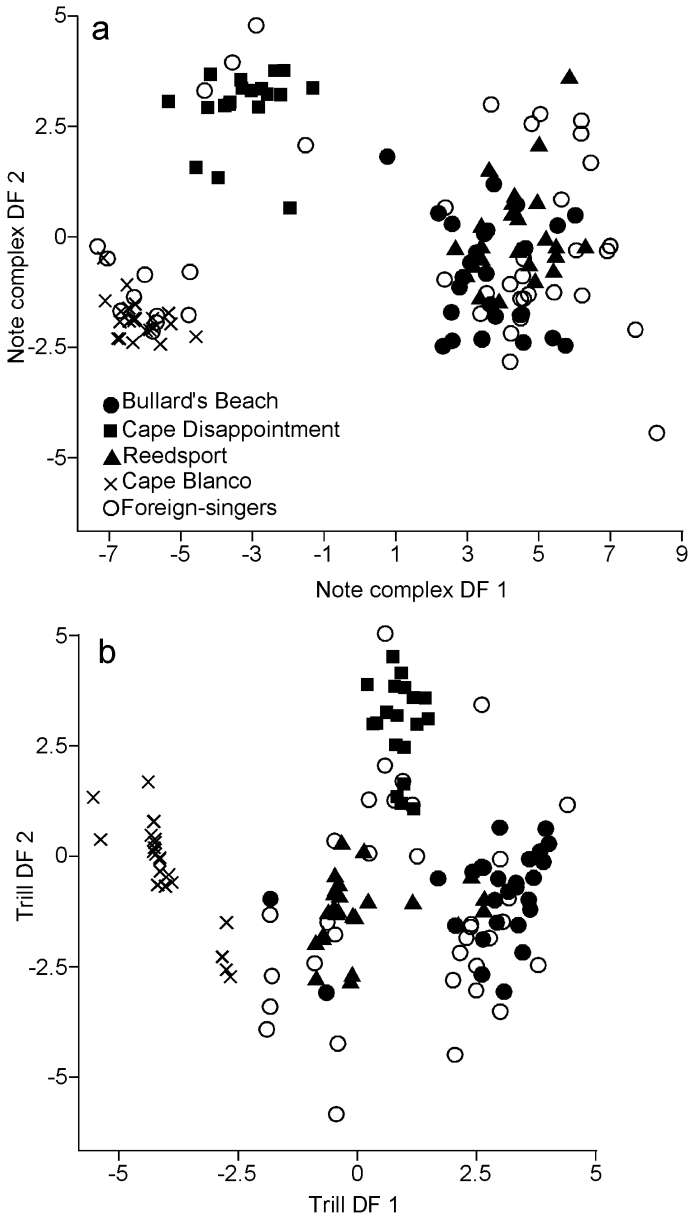


Figure 3. Scatterplots of the first two discriminant functions based on acoustic measurements of (a) note complexes (Table 4) and (b) trills (Table 5) in the model sample of 71 males. Cases are labelled as in Figure 2.

Table 5.

Stepwise discriminant functions analysis of trill acoustic structure in songs in the model sample from four locations ($N = 92$).

| | Function | | |
|----------------------|----------|------|-------|
| | 1 | 2 | 3 |
| Eigenvalue | 6.58 | 2.59 | 0.04 |
| % variance | 72 | 28 | 0.4 |
| Wilks λ | 0.04 | 0.27 | 0.97 |
| Note duration | 0.87 | 0.29 | 0.39 |
| Note elements | -0.75 | 0.30 | 0.59 |
| Note begin frequency | -0.38 | 0.69 | -0.61 |

Functions 1 and 2 are significant ($p < 0.001$). Three of five variables measured were retained in the best model. Values listed for each measurement are the pooled within-groups correlation coefficient between the variable and each function.

probability that their feathers were assigned to a foreign location (Figure 5, Spearman's $\rho = 0.60$, $N = 21$, $p = 0.004$). The correlation remains significant if the three cases of dialect identity disagreement between feathers and song are removed ($\rho = 0.52$, $N = 18$, $p = 0.027$).

3.4. Goal 2: where do males learn their songs?

As described above, 11 foreign-singers had feathers moulted in a foreign location. The 10 remaining foreign-singers that moulted at Bullard's Beach could have learned their foreign dialect from males present in the dialect the

Table 6.

Classification to song dialect based on the acoustic structure of note complexes and trills (in parentheses) in the model sample and the 41 songs in the repertoires of 21 foreign-singers at Bullard's Beach.

| Actual dialect | Predicted dialect | | | |
|---------------------|-------------------|-------------|-----------|---------------------|
| | Bullard's Beach | Cape Blanco | Reedsport | Cape Disappointment |
| Bullard's Beach | 17 (23) | 0 (1) | 7 (1) | 1 (0) |
| Cape Blanco | 0 (0) | 22 (22) | 0 (0) | 0 (0) |
| Reedsport | 9 (5) | 0 (0) | 16 (20) | 0 (0) |
| Cape Disappointment | 0 (0) | 0 (0) | 0 (0) | 19 (19) |
| Foreign-singers | 21 (17) | 11 (0) | 8 (11) | 4 (7) |

Each song in the model sample had one note complex and one trill. Foreign-singers sang a total of 44 note complexes and 35 trills.

previous year. This suggests a minimum of 11 of 21 (52%) of foreign-singers learned their foreign song(s) in a foreign location.

3.5. Goal 3: inter-dialect dispersal

3.5.1. Males at Bullard's Beach

As described above, the males included in the model and foreign-singers samples were chosen on the basis of song, and did not constitute random samples of all yearlings at Bullard's Beach. We approximated a random sample of yearlings by combining the two samples, weighted by their frequency of occurrence. Of the 140 total yearling recruits we observed at Bullard's Beach during the five years between 2004 and 2008, 119 (83%) sang only the local dialect (potential model sample males) while 21 (17%) were foreign-singers. As described above, 5 of 25 model sample males (20%), and 11 of 21 foreign-singers (52%) likely moulted in a foreign location the previous year. The percentage of foreign immigrants among all 140 recruits is therefore 25% ($= 0.83 \times 20\% + 0.17 \times 52\%$), or 5% per year.

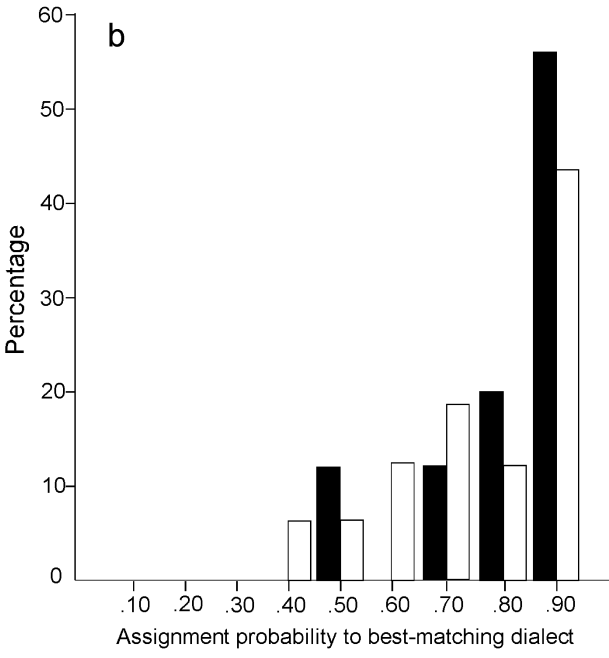
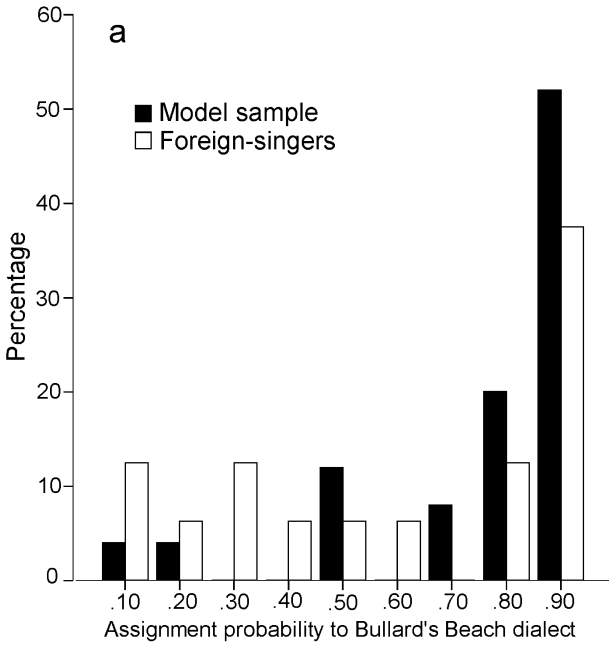
3.5.2. Females at Bullard's Beach

The LDFA model based on feather elements classified 12 of all 35 breeding females (37%) to a foreign location (Table 3). Among 13 likely yearling females, four (31%) were classified to a foreign location, an estimate not different from that for male yearlings (Fisher's exact test, $p = 0.69$). As with males, most female immigrants came from the two dialects bordering the Bullard's Beach dialect: Cape Blanco and Reedsport (Table 3).

4. Discussion

Our main findings are that feathers from different dialect locations differ in their trace element composition, and about half the males that sing songs typical of foreign dialects also have feathers grown in that foreign location the previous year. Males with a larger fraction of foreign dialect song phrases in their song repertoire are more likely to have moulted at a foreign location. We also found that both males and females commonly disperse between dialects. The current analysis extends the findings from Poesel et al. (2008) based on a subset of the data presented here with the analysis of additional samples and a detailed analysis of song structure.

Our main finding that feathers from four spatially separate song dialects differ in their elemental composition assumes that males in the model sample were present at the sample location the previous year when their feathers



were grown. We deliberately biased this sample by only including males that sang songs typical of their respective location. Banding and re-capture the next year of large numbers of individuals are needed to confirm this assumption, but the correct classification of three recaptured males hatched at Bullard's Beach, and the 100% correct classification of 23 chicks sampled in nests at Bullard's Beach are consistent with this assumption, at least for this location. However, 20% of males in the model sample at Bullard's Beach were classified to another location, the result of a combination of measurement error, sampling error and immigration, as discussed below.

We found mixed support for the hypothesis that the 'foreign song' composition of a young male's overproduced song repertoire correlates with the probability that he came from a foreign location. In the majority of cases the independent identifications of a bird's origin based on elemental composition of feathers and song dialect agreed. Males with a larger fraction of their song repertoire composed of foreign dialect(s) had a higher probability of moulting in a foreign location (Figure 5). Arguing against the hypothesis, we found that only a few foreign-singers were classified to a location with a low level of confidence, as would be expected if their feathers blended elements from two locations. Instead, their feathers reflected an origin in either a foreign or the Bullard's Beach dialect. If the body feathers we sampled grow quickly, then there might be insufficient time for them to incorporate elements from more than one location.

Our analyses assume that white-crowned sparrow males are only able to memorize novel song material in their hatching-year summer, as supported by laboratory song learning experiments (Nelson & Marler, 1994; Nelson et al., 1996) and field evidence cited in the Introduction. Males begin to practice song production while on the wintering grounds in California (DeWolfe & Baptista, 1995), but no evidence suggests that they memorize novel song material at that time. If there is a cost to learning song, and since males appear to benefit by breeding in local song neighbourhoods (Poesel et al., 2012; Nelson & Poesel, 2013), then we would not expect selection to favour learning

Figure 4. (a) Histogram of the posterior probability of classification to the Bullard's Beach location based on feather element composition for the 25 males in the model sample (filled bars) and 16 foreign-singers that sang two or more dialects (open bars) at Bullard's Beach. (b) Histogram of the maximum posterior probability of classification to any location for the same two samples of males. Classifications are based on the linear discriminant functions analysis in Table 1.

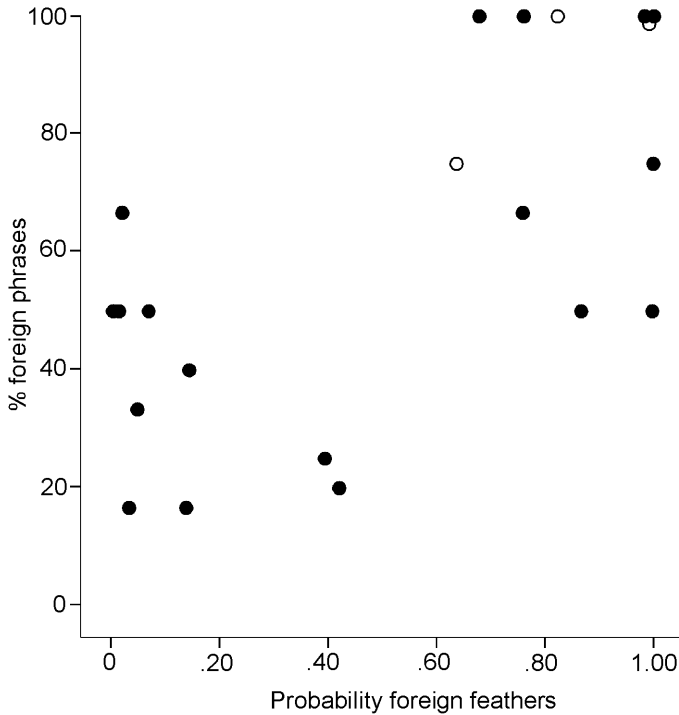


Figure 5. Scatterplot of the percentage of foreign song phrases in the repertoire of 21 foreign-singers at Bullard's Beach versus the posterior probability that their feathers were grown at a foreign location. Open circles represent 3 males for whom the song dialect classification did not agree with the feather locality classification (see text).

from non-territory neighbours on the wintering grounds as the vocal dialects are not geographically segregated in winter (DeWolfe & Baptista, 1995). Rising testosterone titres induced by increased day lengths appear to induce song production, but inhibit song memorization in late winter (Whaling et al., 1998).

We did not measure natal dispersal in this study, but rather dispersal from where the bird was during body moult the previous summer. It would be interesting to compare the element profiles of flight feathers, which are largely grown in the nest and are not moulted until after the first breeding season, to body feathers of the first basic plumage, which are grown several months later. The flight feathers should correlate with natal origin while the body feathers should reflect any later dispersal movements. Some yearling males and females may have already undergone some dispersal movement prior to

body moult, as seems likely from Morton et al.'s (1991) observation in *Z. l. oriantha* of a large mid-summer influx of hatching-year males hatched outside the study area. If males learned song prior to beginning moult, then their feather element signature would not match the dialect(s) they expressed. It is possible that some of the males in the model sample that were assigned to a foreign location based on feather composition learned the local dialect, moved to a foreign dialect in late summer where they moulted, but then returned to their natal location to breed. Such movements may represent prospecting for a suitable breeding territory by young birds (Reed et al., 1999; Dittmann et al., 2005). We have suggested that males may wander in their hatching-year summer, as documented in *Z. l. oriantha* (Morton et al., 1991; Morton, 1992), and learn several vocal dialects while prospecting for a breeding territory (Nelson & Poesel, 2009, 2014). Learning two or more vocal dialects might increase a male's chances of sharing song with neighbours if the future breeding site cannot be predicted.

We compared estimates of dispersal probability for males and females. In most bird species females are more likely to disperse and disperse longer distances than males (Clarke et al., 1997; Mabry et al., 2013). In our small sample, both sexes were equally likely to disperse, a result also found in *Z. l. oriantha* based on band-recapture data (Morton, 1992). This is not uncommon, as no sex difference in either distance or probability of natal dispersal is found in 40% of bird species (Clarke et al., 1997). We emphasize again that we did not measure natal dispersal directly as banding studies have done, and so comparisons should be made cautiously. As found in other species, both sexes were more likely to disperse from two neighbouring locations than from a distant location (Paradis et al., 1998), although our estimates are truncated by limited sampling (Koenig et al., 1996). Occasional long-distance dispersal does occur however, as several males and females apparently dispersed 160–348 km, the range of the Cape Disappointment dialect from Bullard's Beach. These individuals may cut short their northward spring migration if they find a vacant territory south of where they moulted the previous summer. Early in spring we commonly heard males in small flocks quietly singing dialects that occur north of Bullard's Beach before they moved on.

Errors in classifying birds to moult area based on feather composition may arise from spatial heterogeneity in element profiles within dialect areas. We only sampled a single location within each dialect; it is unknown whether

element profiles vary over small distances within dialects. The dialects represented at Bullard's Beach, Cape Blanco and Reedsport are comparatively small, and range 40–50 km along the coast, so such error may be relatively small in these dialects (Figure 1). The dialect at Cape Disappointment on the other hand, extends 190 km south to Newport, Oregon and encompasses multiple river drainages which might produce spatial heterogeneity in the distribution of trace elements within the dialect (Gaillardet et al., 2003). However, the strong agreement between independent classifications based on feather elements and song dialect structure (86% of 21 foreign-singers) suggests that the distributions of trace elements and song dialects are broadly concordant, at least within this region of the coast. Denser sampling might improve this agreement. Another source of error may be introduced by temporal variation. The samples at Bullard's Beach were collected over a five-year-long period, and it is possible that element profiles may vary over time. Our samples are too small to have adequate power to detect such an effect if it exists. A study by Szep et al. (2003) indicates trace element profiles are stable across years in one species.

Despite the various sources of error discussed above, differences in trace element markers combined with song data suggests that considerable movement, about 5% per year, occurs by males and females among dialect areas in the Puget Sound white-crowned sparrow. Our evidence of frequent movement of both males and females among dialects, some of which presumably represents natal dispersal, agrees with genetic evidence that the population of the Puget Sound white-crowned sparrow is essentially panmictic (Soha et al., 2004; Poesel et al., in press).

Acknowledgements

We thank Anthony Lutton for advice in using the ICP-MS. Two reviewers made helpful comments on the manuscript. We thank the NSF (IBN04-15842 and REU DBI-0846354) for support, and the Oregon State Parks Department, and the Port of Bandon for granting permission to work on their properties. Procedures were approved by Ohio State University IACUC Protocol 2000A005. Sample collection complied with the current laws of Oregon, Washington and the USA.

References

- Adout, A., Hawlena, D., Maman, R., Paz-Tal, O. & Karpas, Z. (2007). Determination of trace elements in pigeon and raven feathers by ICPMS. — *Int. J. Mass Spectrometr.* 267: 109–116.
- Anderson, K.E., Rothstein, S.I., Fleischer, R.C. & O’loghlen, A.L. (2005). Large-scale movement patterns between song dialects in brown-headed cowbirds (*Molothrus ater*). — *Auk* 122: 803–818.
- Baker, M.C. & Mewaldt, L.R. (1978). Song dialects as barriers to dispersal in white-crowned sparrows, *Zonotrichia leucophrys nuttalli*. — *Evolution* 32: 712–722.
- Baptista, L.F. (1977). Geographic variation in song and dialects of the Puget Sound white-crowned sparrow. — *Condor* 79: 356–370.
- Beecher, M.D., Campbell, S.E. & Stoddard, P.K. (1994). Correlation of song learning and territory establishment strategies in the song sparrow. — *Proc. Natl. Acad. Sci. USA* 91: 1450–1454.
- Beecher, M.D., Campbell, S.E. & Nordby, J.C. (2000). Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. — *Anim. Behav.* 59: 29–37.
- Bjerke, T.K. & Bjerke, T. (1981). Song dialects in the redwing *Turdus iliacus*. — *Ornis Scand.* 12: 40–50.
- Bradley, R.A. (1994). Cultural change and geographic variation in the songs of the belding’s savannah sparrow (*Passerculus sandwichensis beldingi*). — *Bull. S. Calif. Acad. Sci.* 93: 91–109.
- Briskie, J.V. (1999). Song variation and the structure of local song dialects in the polygynandrous Smith’s longspur. — *Can. J. Zool.* 77: 1587–1594.
- Catchpole, C.K. & Slater, P. (2008). *Bird song*. — Cambridge University Press, Cambridge.
- Clarke, A.L., Sæther, B.E. & Røskaft, E. (1997). Sex biases in avian dispersal: a reappraisal. — *Oikos* 79: 429–438.
- Conrads, K. (1976). Studien an Fremddialekt-Sängern und Dialekt-Mischsängern des Ortolans (*Emberiza hortulana*). — *J. Ornithol.* 117: 438–450.
- Cunningham, M.A., Baker, M.C. & Boardman, T.J. (1987). Microgeographic song variation in the Nuttall’s white-crowned sparrow. — *Condor* 89: 261–275.
- Dewolfe, B.B. & Baptista, L.F. (1995). Singing behavior, song types on their wintering grounds and the question of leap-frog migration in Puget Sound white-crowned sparrows. — *Condor* 97: 376–389.
- Dittmann, T., Zinsmeister, D. & Becker, P.H. (2005). Dispersal decisions: common terns, *Sterna hirundo*, choose between colonies during prospecting. — *Anim. Behav.* 70: 13–20.
- Donovan, T., Buzas, J., Jones, P. & Lisle Gibbs, H. (2006). Tracking dispersal in birds: assessing the potential use of elemental markers. — *Auk* 123: 500–511.
- Engineering Design (2009). *Signal Reference Guide*. — Engineering Design, Berkeley, CA.
- Gaillardet, J., Viers, J. & Dupre, B. (2003). Trace elements in river waters. — In: *Surface and ground waters, weather and soils* (Drever, J.I., ed.). Elsevier, Oxford, p. 225–272.

- Glaubrecht, M. (1991). Gesangsvariation der Goldammer (*Emberiza citrinella*) in Norddeutschland und auf den dänischen Inseln. — *J. Ornithol.* 132: 441-445.
- Gómez-Díaz, E. & González-Solís, J. (2007). Geographic assignment of seabirds to their origin: combining morphologic, genetic, and biogeochemical analyses. — *Ecol. Appl.* 17: 1484-1498.
- Greenwood, P.J. & Harvey, P.H. (1982). The natal and breeding dispersal of birds. — *Annu. Rev. Ecol. Syst.* 13: 1-21.
- Grinnell, J. (1928). Notes on the systematics of West American birds. III. — *Condor* 30: 185-189.
- Hegelbach, J. (1986). Gesangsdialekt und Fortpflanzungserfolg bei Grauammer—male *Emberiza calandra*. — *Ornithol. Beobacht.* 83: 253-256.
- Kelsall, J.P. & Burton, R. (1979). Some problems in identification of origins of lesser snow geese by chemical profiles. — *Can. J. Zool.* 57: 2292-2302.
- Koenig, W.D., Van Vuren, D. & Hooge, P.N. (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. — *Trends Ecol. Evol.* 11: 514-517.
- Mabry, K.E., Shelley, E.L., Davis, K.E., Blumstein, D.T. & Van Vuren, D.H. (2013). Social mating system and sex-biased dispersal in mammals and birds: a phylogenetic analysis. — *PLoS ONE* 8: e57980.
- McGregor, P.K. (1980). Song dialects in the corn bunting (*Emberiza calandra*). — *Z. Tierpsychol.* 54: 285-297.
- Mewaldt, L.R. & King, J.R. (1978). Latitudinal variation of postnuptial molt in Pacific coast white-crowned sparrows. — *Auk* 95: 168-179.
- Morrison, D.G. (1969). On the interpretation of discriminant analysis. — *J. Market. Res.* 6: 156-163.
- Morton, M.L. (1992). Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain white-crowned sparrow. — *Condor* 94: 117-133.
- Morton, M.L. (2002). The mountain white-crowned sparrow: migration and reproduction at high altitude. — *Stud. Avian Biol.* 24: 1-236.
- Morton, M.L., Wakamatsu, M.W., Pereyra, M.E. & Morton, G.A. (1991). Postfledging dispersal, habitat imprinting, and philopatry in a montane, migratory sparrow. — *Ornis Scand.* 22: 98-106.
- Nathan, R., Perry, G., Cronin, J.T., Strand, A.E. & Cain, M.L. (2003). Methods for estimating long-distance dispersal. — *Oikos* 103: 261-273.
- Nelson, D.A. (1999). Ecological influences on song learning in the white-crowned sparrow. — *Anim. Behav.* 58: 21-36.
- Nelson, D.A. (2000). Song overproduction, selective attrition, and vocal dialects in the white-crowned sparrow. — *Anim. Behav.* 60: 887-898.
- Nelson, D.A. (2017). Geographic variation in song phrases differs with their function in white-crowned sparrow song. — *Anim. Behav.* 124: 263-271.
- Nelson, D.A. & Marler, P. (1994). Selection-based learning in bird song development. — *Proc. Natl Acad. Sci. USA* 91: 10498-10501.

- Nelson, D.A. & Poesel, A. (2007). Segregation of information in a complex acoustic signal: individual and dialect identity in white-crowned sparrow song. — *Anim. Behav.* 74: 1073-1084.
- Nelson, D.A. & Poesel, A. (2009). Does learning produce song conformity or novelty in white-crowned sparrows? — *Anim. Behav.* 78: 433-440.
- Nelson, D.A. & Poesel, A. (2013). Song sharing correlates with pairing success, but not territory tenure in the Puget Sound white-crowned sparrow. — *Behav. Ecol. Sociobiol.* 67: 993-1000.
- Nelson, D.A. & Poesel, A. (2014). Tutor choice and imitation accuracy during song learning in a wild population of the Puget Sound white-crowned sparrow. — *Behav. Ecol. Sociobiol.* 68: 1741-1752.
- Nelson, D.A., Marler, P. & Morton, M.L. (1996). Overproduction in song development: an evolutionary correlate with migration. — *Anim. Behav.* 51: 1127-1140.
- Nelson, D.A., Hallberg, K.I. & Soha, J.A. (2004). Cultural evolution of Puget Sound white-crowned sparrow song dialects. — *Ethology* 110: 879-908.
- Norris, D.R., Lank, D.B., Pither, J., Chipley, D., Ydenberg, R.C. & Kyser, T.K. (2007). Trace element profiles as unique identifiers of western sandpiper (*Calidris mauri*) populations. — *Can. J. Zool.* 85: 579-583.
- O’Loughlen, A.L. & Rothstein, S.I. (1993). An extreme example of delayed vocal development: song learning in a population of wild brown-headed cowbirds. — *Anim. Behav.* 46: 293-304.
- Óvári, M., Laczi, M., Török, J., Mihucz, V.G. & Zárny, G. (2016). Elemental composition in feathers of a migratory passerine for differentiation of sex, age, and molting areas. — *Environm. Sci. Poll. Res.*: 1-14.
- Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R. (1998). Patterns of natal and breeding dispersal in birds. — *J. Anim. Ecol.* 67: 518-536.
- Payne, R.B., Payne, L.L. & Doehlert, S.M. (1988). Biological and cultural success of song memes in indigo buntings. — *Ecology* 69: 104-117.
- Poesel, A., Nelson, D.A., Gibbs, H.L. & Olesik, J.W. (2008). Use of trace element analysis of feathers as a tool to track fine-scale dispersal in birds. — *Behav. Ecol. Sociobiol.* 63: 153-158.
- Poesel, A., Nelson, D.A. & Gibbs, H.L. (2012). Song sharing correlates with social but not extrapair mating success in the white-crowned sparrow. — *Behav. Ecol.* 23: 627-634.
- Poesel, A., Fries, A., Miller, L., Gibbs, H.L., Soha, J.A. & Nelson, D.A. (in press). Evidence for gene flow among song dialects of the Puget Sound white-crowned sparrow. — *Ethology*.
- Pyle, P., Howell, S.N.G., Yunick, R.P. & Desante, D.F. (1987). Identification guide to North American Passerines. — Slate Creek Press, Bolinas, CA.
- Reed, J.M., Boulonier, T., Danchin, E. & Oring, L.W. (1999). Informed dispersal. Prospecting by birds for future breeding sites. — In: (Nolan, V., Ketterson, E.D. & Thompson, C.F., eds). Springer, Boston, MA, p. 189-259.
- Soha, J.A., Nelson, D.A. & Parker, P.G. (2004). Genetic analysis of song dialect populations in Puget Sound white-crowned sparrows. — *Behav. Ecol.* 15: 636-646.

- Szép, T., Møller, A.P., Vallner, J., Kovács, B. & Norman, D. (2003). Use of trace elements in feathers of sand Martin *Riparia riparia* for identifying moulting areas. — *J. Avian Biol.* 34: 307-320.
- Trainer, J.M. (1989). Cultural evolution in song dialects of yellow-rumped caciques in Panama. — *Ethology* 80: 190-204.
- Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. (2002). Links between worlds: unraveling migratory connectivity. — *Trends Ecol. Evol.* 17: 76-83.
- Whaling, C.S., Soha, J.A., Nelson, D.A., Lasley, B. & Marler, P. (1998). Photoperiod and tutor access affect the process of vocal learning. — *Anim. Behav.* 56: 1075-1082.