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METHODS

Use of trace element analysis of feathers as a tool to track fine-scale dispersal in birds

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Abstract Tracking dispersal and migratory movements of animals over small and large spatial scales is a challenge. In birds, a promising yet underutilized tool is the trace elemental composition of feathers. The elemental profile of a feather may reveal information about the geographic origin of a bird provided that molting occurs on the breeding grounds and that elemental differences exist between breeding areas. Here, we explore the use of trace elemental composition in body feathers of the Puget Sound white-crowned sparrow *Zonotrichia leucophrys pugetensis* as a tool (1) to discriminate among birds collected in four different song dialect populations along a 400-km stretch of the Pacific Northwest coast and (2) to assign males singing nonlocal dialects in one population to potential natal populations. Inductively coupled plasma mass spectrometry detected 34 trace elements in sampled feathers and in a discriminant function analysis seven of these elements differed among the four source populations. Half of the six nonlocal dialect singers, who were likely to have immigrated into the focal population, were assigned to a population that matched their song dialect. Our study suggests that feather microchemistry is a promising tool for identifying geographic origins of dispersing birds over small geographic scales and in combination with other markers, such as song, may give insight into ecological and evolutionary processes.

Keywords Trace elements · Fine-scale dispersal · Song dialect · *Zonotrichia leucophrys*

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Introduction

Tracking large- and small-scale movements and determining natal origins of individual animals is a great challenge to behavioral ecologists and conservation biologists (e.g., Nathan 2001; Akesson 2002; Webster et al. 2002). Dispersal of organisms influences population dynamics and may ultimately affect evolutionary patterns, i.e., gene flow and genetic structuring of subpopulations (Tilman and Kareiva 1997). In a world where habitats are increasingly fragmented, migration and dispersal patterns of organisms may have important implications for conservation efforts (see Moore et al. 1995).

In birds, dispersal has traditionally been studied by tracking the movements of tagged individuals. This has severe limitations because of the difficulties of detecting small numbers of marked individuals (Webster et al. 2002). As a result, there has been great interest in exploring the use of alternative methods that rely on the genetic and/or biogeochemical composition of individuals since all individuals contain such signatures whereas only a fraction can be marked with tags in a given study (see Rubenstein and Hobson 2004). Biogeochemical markers such as stable isotopes and trace elements are derived from elements in the environment that enter the water and food chain and are incorporated into animal tissues. Concentrations in these tissues then reflect environmental elemental concentrations. Prerequisites to identifying the geographic origin of a sample in an elemental analysis are that tissues are synthesized at the particular location of interest, that elemental concentrations once incorporated into a certain tissue cannot be altered by environmental or physiological effects, and that elemental abundances show geographic patterns in the environment (see below). Fish otoliths and bird feathers are promising tissues for such analyses (examples in Rubenstein and Hobson 2004).

Among stable isotopes, deuterium (δD), carbon (δ^{13}C), nitrogen (δ^{15}N), and strontium (δ^{87}Sr) vary in predictable patterns across environments that can be related to precipitation, food, or soil substrate, respectively (e.g., Chamberlain et al. 1997; Kelly and Finch 1998). However, isotopic variation mainly occurs at a continental or regional (>1,000 km) scale (Marra et al. 1998) and allows tracking of animal movements between different ecosystems or ecoregions (Hobson 1999). However, this scale of differentiation is too coarse for many studies of dispersal over finer geographic scales, and thus there is a significant need for other biogeochemical markers that show differentiation over smaller geographic distances.

Here, we show that the analysis of trace elements shows potential as a marker system for tracking fine-scale dispersal in birds. Trace elements are generated from underlying bedrocks by pedogenic processes and may reflect effects of external factors, such as flooding events or forest fires (Kabata-Pendias and Pendias 2001). In fish, trace elements are continuously incorporated into a carbon backbone in ear bones (otoliths), and this elemental composition has been used to differentiate among local spawning populations and to identify origins of recruits (see Campana 1999). In birds, trace elements from the environment are incorporated into feathers during growth. To date, using trace elements as markers of movement in birds has given mixed results: two studies successfully identified molting areas and assigned individuals to source populations (Szep et al. 2003; Gomez-Diaz and Gonzalez-Solis 2007), while another study did not (Donovan et al. 2006).

We report here the successful application of trace element profiles in feathers of the white-crowned sparrow (hereafter WCSP) *Zonotrichia leucophrys* to study dispersal among populations within 400 km of each other. Dispersal in this species is of particular interest since it may influence song acquisition and song use in males. The Puget Sound WCSP *Z. leucophrys pugetensis* inhabits coastal dunes and forest openings along the Pacific Northwest coast of America. Thirteen song dialects (d1–13) have been described among populations within

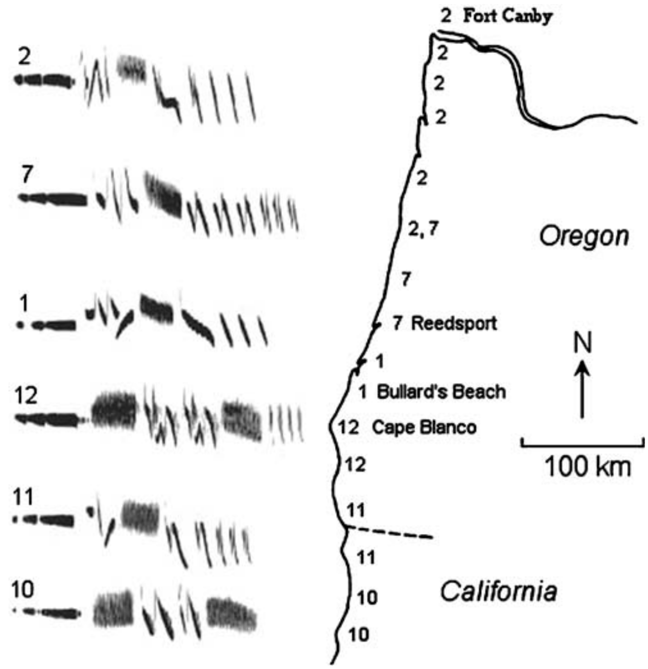

Fig. 1 Map of the Pacific Northwest coast showing six out of 13 song dialects in the Puget Sound white-crowned sparrow *Z. leucophrys pugetensis* (modified from Nelson et al. 2004). The *numbers* refer to locations where different dialects (d10, 11, 12, 1, 7, 2 from south to north) occur and are illustrated by sonograms on the *left*. We collected feathers from birds at Cape Blanco, Bullard's Beach, Reedsport, and Fort Canby and from nonlocal dialect singers at Bullard's Beach

this subspecies' range from northern California to southern British Columbia (Fig. 1; Baptista 1977; Nelson et al. 2004). These dialects are a consequence of song learning by males during their first summer (Marler 1970; Nelson 2000) and a subsequent return to breed near the site of learning by most males. Male WCSP often memorize and sing more than one dialect, i.e., overproduce, at the beginning of their first breeding season before they crystallize a single dialect which resembles the dialect sung by most of their territorial neighbors (Nelson 2000). This ability to change song after dispersal and the fact that some males learn two or more dialects during the sensitive phase for song learning (Chilton and Lein 1996) mean that song dialect is not an infallible index of where a male spent his natal summer.

In this study, we used trace elements in feathers to track the natal origin of foreign dialect singers in a mixed-dialect population of WCSP to provide an independent test of whether these males had learned their songs elsewhere. We analyzed trace elemental compositions in body feathers of the WCSP to determine if feather elemental profiles (1) differ among birds collected in four different song dialect populations along the Pacific Northwest coast and (2) could be used to assign males singing nonlocal dialects to the geographic location of feather molt.

Materials and methods

We collected feathers from 26 male *Z. leucophrys pugetensis* in four different dialect populations along a 400-km stretch of the Oregon, USA coast (Fig. 1). The sites sampled from south to north were Cape Blanco State Park (42° 50′ 54″ N 124° 33′ 25″ W), Bullard's Beach State Park (43° 7′ 26″ N 124° 25′ 26″ W), Reedsport (43° 41′ 56″ N 124° 6′ 44″ W), and Fort Canby (46° 8′ 1″ N 123° 52′ 39″ W). 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.

The Puget Sound WCSP has a complete molt of body and flight feathers on the breeding grounds starting in mid-July prior to the migration south (Lewis 1975). This subspecies also molts the head feathers and some body and flight feathers (the central pair of tail feathers and secondary flight feathers 7–9) in late winter and early spring (Blanchard 1941; Banks 1964). In this study, we analyzed two or three flank feathers, which were initially collected for a different purpose. To address concerns about whether flank feathers were molted on the wintering grounds in addition to the breeding grounds, we examined 80 specimens collected between January and mid-April in the collection of the Museum of Vertebrate Zoology, University of California, Berkeley, including many of the specimens examined by Blanchard and Banks. Seven of the April specimens were collected on the breeding grounds while all others came from the wintering grounds in central California. Using a probe, we examined the crown, breast, and flanks for the presence of sheathed feathers which would indicate a molt in progress. We also recorded whether the two central tail feathers appeared new or were growing and whether secondaries 7–9 were molting.

In the field, we caught males between April and June by broadcasting WCSP song from a loudspeaker in front of a mist net. Strong territorial responses indicated that the sampled males were resident, and many were mated. All of these males at each location sang the local dialect; we thus assume that they had likely molted at the given site the previous summer. We collected two to three flank feathers and stored them in sealed and labeled plastic bags until we analyzed them in the laboratory.

We collected feathers from an additional six territorial males at Bullard's Beach State Park that sang nonlocal dialects. Three of these males could be identified as yearlings based on the retention of brown feathers in their crown from their first basic plumage (Blanchard 1941). The other three males had complete adult crowns but occupied territories held the previous year by a banded bird who did not return. We thus assume that they were also likely yearlings. These six males had presumably spent at least part of the previous summer in a different area where they had also learned their songs.

Song dialects were identified from recordings made with a Marantz PMD670 solid-state recorder (Marantz Professional, Kanagawa, Japan) sampling at 48 kHz, 16-bit amplitude resolution, and Sennheiser MKH70 or ME67 "shotgun" microphones (Sennheiser, Wedemark, Germany) and Rycote windscreens (Rycote Ltd., Stroud, UK).

Trace element analysis

To measure trace elements in feather samples, we followed Donovan et al. (2006) and used inductively coupled plasma mass spectrometry (ICP-MS) for a semiquantitative 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 100°F, and 2 mg of feathers from each individual weighed out to the nearest 0.1 mg in a 15- or 50-ml polyethylene test tube. One milliliter of concentrated, purified nitric acid was added and tubes were immersed in boiling water for 6 min or until the feathers had entirely dissolved. Once cooled, we added distilled, deionized water to the 10-ml mark.

We used a PerkinElmer Sciex ELAN 6000 ICP-MS to analyze the prepared samples and normalized intensities for isotopic abundance. Since we did not know the elemental composition of the collected feathers, we performed a semiquantitative analysis for unknown solutions with TotalQuant III software. A complete spectrum from 6 to 240 m/z (with the exception of 16–18, 40–41, 211–229, which were skipped) was measured for a blank, a single standard solution containing a subset of the elements of interest and for each sample. Reference response factors for each element that accounted for isotope patterns, degree of ionization, and spectrometer mass bias were provided by the manufacturer. Measurement of a single standard was used by the software to update the response factors shortly before samples were measured. The TotalQuant semiquantitative analysis software uses the response factors, isotopic patterns for each element, a database of molecular ions that could cause spectral overlaps, and heuristic rules to determine the contribution of each element in the sample to the measured spectrum. In this way, the concentrations of up to 70 elements can be estimated even if the element is not in the standard solution. We calibrated the instrument with a standard solution containing 10 ppb of Ag, Al, As, Br, Be, Cd, Co, Cr, Cu, Mn, Mo, Pb, Sb, Sl, Tl, Th, U, V, and Zn and 100 ppb of Ni. We analyzed the following 70 elements: Ag, Al*, As*, Au, Ba, Bi, Br, Ca, Cd*, Ce*, Cl, Co*, Cr, Cs, Cu*, Dy, Er, Eu, Fe*, Ga*, Gd, Ge*, Hf, Hg, Ho, I*, In*, Ir, K*, La*, Lu, Mg*, Mn*, Mo*, Na, Nb*, Nd*, Ni*, Os, P, Pb, Pd, Pr, Pt, Rb*, Re, Rh, Ru*, S, Sb*, Sc*, Se*, Si, Sm, Sn*, Sr*, Ta, Tb, Te, Th*, Ti*, Tl*, Tm, U*, V*, W, Y*, Yb, Zn*, and Zr*. Thirty-four elements with asterisks were present in some feather samples, could be measured reliably, and were thus included in further analyses.

Statistical analyses

Analyses were performed in SPSS 15.0. We performed forward stepwise linear discriminant function analysis on untransformed concentration values of 34 elements in the 26 males in the training sample to investigate whether trace elements differed among geographic locations. We calculated Wilks' lambda; variables with F=3.84 entered the model and variables with F=2.71 were removed. Using the seven elements selected in the training sample, we then classified the six individuals with nonlocal song dialects to one of the four source populations. In classifying cases to geographic location, we assumed prior probabilities of group membership to be equal.

Results

In terms of feather molt, 59 of 80 (74%) museum specimens had been molting at least one feather tract, most commonly in February and March, while 23 (29%) specimens showed evidence of molt in the chin or upper breast regions. However, most relevant to our feather sampling protocol, only three skins (4%) had any pin feathers on the flanks near where we collected feathers in the field. We discuss below the implications of the light molt of flank feathers in late winter.

Thirty-four trace elements were present at a concentration of ≥100 ppb in at least one feather sample (see elements marked with asterisks in the list above). A stepwise linear discriminant function analysis using three functions based on seven trace elements correctly assigned 100% (jackknifed classifications) of the 26 individuals in the training sample to their sample location (Fig. 2; Wilks' λ=0.001, 0.02, 0.19, χ^2=135.4, 76.1, 32.5, df=21, 12, 5, all p<0.001). The first function explained 61.2% of the total variance among locations and correlated positively with strontium, magnesium, and yttrium and negatively with iodine. The second function explained 25.6% and correlated negatively with zinc. The third function explained 13.2% and correlated positively with gallium and negatively with neodymium.

None of the six males that sang nonlocal dialects at Bullard's Beach State Park was assigned to the population of residence. Two males that sang dialect 7 were assigned to Reedsport, where dialect 7 occurs; one male that sang dialect 12 was assigned to Cape Blanco where dialect 12 occurs and the other three males, two of which sang dialect 2 and one sang dialect 7, were also assigned to Cape Blanco (dialect 12; Fig. 2). The average posterior probability of group classification for each of these six males was 96.1% (min 80.5–max 100%) suggesting that none of the classifications were "borderline" cases, with feather elemental compositions similar to a location other than the one assigned.

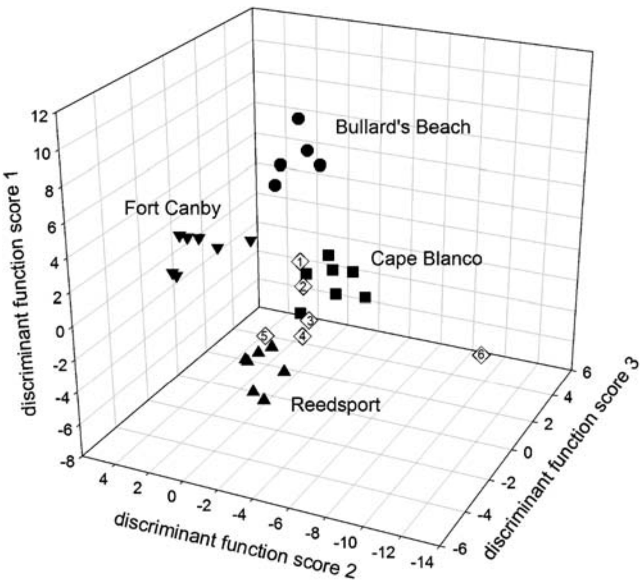

Fig. 2 Scores from a linear discriminant function analysis based on seven trace elements (Sr, Mg, Y, I, Zn, Ga, Nd) in body feathers of the Puget Sound white-crowned sparrow *Z. leucophrys pugetensis*. *Circles* represent five individuals from Bullard's Beach, *downward triangles* seven individuals from Fort Canby, *upward triangles* seven individuals from Reedsport, and *squares* seven individuals from Cape Blanco; *diamonds* with *numbers* represent six individual males singing nonlocal dialects at Bullard's Beach (see "Materials and methods" for further details)

Discussion

Our key result is that we found distinct trace element profiles in feathers of adult WCSP captured at each of four sampling locations as close as 40 km apart. This suggests that trace elemental profiles differ between closely spaced populations in a terrestrial passerine bird and can potentially be used to study dispersal movements. These results are comparable to an elemental analysis of feathers in *Calonectris* shearwaters (Gomez-Diaz and Gonzalez-Solis 2007) where birds could be assigned to breeding colonies at specific islands based on trace elemental composition. The magnitude of differentiation that we detected in the Puget Sound WCSP was much greater (100% differentiation among locations) than in the shearwaters even though it was at a smaller geographic scale.

It is possible that a few of the flank feathers that we analyzed were molted on the wintering grounds or during the northward spring migration instead of on the breeding grounds the previous summer. If flank feathers were commonly molted in late winter, to explain the geographic differences in elemental composition of feathers found here, we would have to postulate that birds from different breeding areas also spend the winter in separate areas, but this is not the case. DeWolfe and Baptista (1995) studied *Z. leucophrys pugetensis* on the wintering grounds at five locations in California. They found that individuals in the wintering flocks at each site sang two to seven different dialects, including three of the dialects we sampled in this study. We conclude that the differences in elemental composition of feathers reflect spatial variation in feathers grown primarily on the breeding grounds.

Environmental differences in trace elements

The effectiveness of trace element analyses in tracking the origins of organisms depends on underlying differences in the environment that are incorporated into the food chain. We suspect that our success at detecting differentiation in elemental composition among WCSP populations at a fine geographic scale is based on each of the four sampled locations occurring at the mouth of a different river. The abundance of trace elements in rivers may be influenced by microclimatic conditions and human impacts which are likely to vary over short distances (see Gaillardet et al. 2003). Also, the four watersheds corresponding to our sample sites are likely to drain geologically dissimilar regions. The Columbia river is the only river of the four draining areas inland of the Coast range. The Sixes watershed encompasses the hard bedrock of the Klamath Mountains, and Umpqua and Coquille watersheds both drain mountains formed of old marine sediments (Oregon Sea Grant 2003).

In aquatic habitats, some patterns of specific trace elements have been detected and are incorporated into animal tissues. The concentration of strontium (Sr) in seawater is over one order of magnitude greater than in freshwater (Ingram and Sloan 1992), and this difference can be used, for example, to track fish migrations from freshwater to sea and vice versa (e.g., Secor et al. 1995). Terrestrial gradients in trace elements are poorly known, and this may explain the mixed results of previous studies in detecting geographic differences. In the sand martin *Riparia riparia*, Szep et al. (2003) found large differences in the composition of feathers grown in Africa versus Europe where food sources are likely to differ in their elemental composition over this large geographic scale. Similarly, Donovan et al. (2006) could discriminate among feathers collected at sites more than 1,200 km apart but not among geographically neighboring sites, for example, within the state of Wisconsin, USA. WCSP are omnivorous and show seasonal changes in their food uptake including seeds, plant material, and insects (Morton 1967). However, at the end of the breeding season when birds molt their body feathers, we assume that all birds utilize similar food sources which will lead to an uptake of similar trace elements into their growing feathers but different among geographic locations. Also, WCSP depend on a steady supply of drinking water which will contain trace elements from the environment (MacMillen and Snelling 1966). Differences in elemental composition among rivers have been used in fisheries to assign fish to their natal river (e.g., Thorrold et al. 1998). In sum, we speculate that elemental analyses in birds may be most useful for fine-scale estimates of dispersal when populations of interest are associated with distinct aquatic habitats such as rivers or lakes which have distinct watersheds.

Trace elements as a tool in studies of dispersal

We could successfully exclude six nonlocal dialect singers from their breeding location and assign them to a neighboring site. This suggests that these males had learned their song(s) in a different population and immigrated into the sample population. Half of the six nonlocal dialect singers were assigned to a population that matched their song dialect. These males had presumably learned their songs in the area they were assigned to the previous summer and had then immigrated into the focal population at Bullard's Beach. The other nonlocal dialect singers may have been misassigned since their song did not match the dialect of the assigned population. We did not sample every possible site within the males' potential natal dialects (Fig. 1) and there may have been fine-scale geographic differences in trace elemental composition that we did not detect. Another factor contributing to these apparent classification errors is that males in their first summer may wander among several dialects and learn two or more dialects, as shown by three males in this study. They sang two dialects that were not adjacent (dialects 1 and 2 and dialects 7 and 12; Fig. 1), and thus they could not likely have learned these in one location. The feather composition of yearlings could conceivably reflect the uptake of elements from several different locations, depending on how long a bird spent in each location and what stage of molt it was in. Such "mixing" of elements from several locations may explain in part why only one of the three yearling males that sang two dialects (d7 and 12) was correctly assigned to one of the dialects he sang (d7). In the mountain WCSP *Z. leucophrys oriantha*, Morton et al. (1991) reported a late-season influx of juvenile birds that were hatched off the study site. These juveniles were in molt, and many returned as breeders the next year. Similar movements may occur in *Z. leucophrys pugetensis*.

In the Puget Sound WCSP, the trace elemental composition of feathers may provide a "signature" of where a bird spent the previous summer and thus can be used to track dispersal and exposure to tutor songs. Male songbirds may adjust their use of learned songs to their social environment on the breeding grounds after dispersal by selective attrition (Nelson 2000; Nordby et al. 2007). These processes may obscure the male's natal origin and here trace elemental profiles in feathers may be useful to track geographic origins.

To conclude, trace element analysis of feathers may provide a promising tool for identifying geographic origins of dispersing birds over small geographic scales given that elements in the environment differ on the same scale. In songbirds, tracking natal origins of males and females will give insight into song-learning processes in the wild. A combination of biogeochemical markers and behavioral traits may give insight into ecological and evolutionary processes.

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