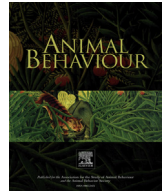




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## Geographical variation in song phrases differs with their function in white-crowned sparrow song

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Complex signals that convey diverse forms of information may face conflicting pressures on their structure. Certain messages, such as species identification or 'alerting' receivers may require a relatively invariant signal structure, while messages about dialect or individual identity and motivation require structural diversity within and among individuals of a species. A resolution to this conflict is to encode different messages in different parts of the signal. When the signal is learned, as in birdsong, parts of the signal may develop along differing developmental pathways in order to produce the necessary signal variation. I tested the hypothesis that three phrases in the song of the Puget Sound white-crowned sparrow, *Zonotrichia leucophrys pugetensis*, that are inferred to convey different messages will vary in their patterns of geographical variation along a 560 km long transect of the Pacific northwest coast of North America. I measured acoustic features of the songs of 267 males and tested for geographical structure using Mantel tests and Mantel correlograms. As predicted, the introductory whistle phrase, inferred to have an 'alerting' function, was geographically invariant. In contrast, the note complex and trill phrases, which convey information about individual identity and geographical origin, both decreased in similarity between males as distance increased. The two phrases have somewhat independent patterns of geographical variation. I suggest that differences in how these phrases develop, as measured in laboratory song-learning experiments, coupled with dispersal may contribute to the differing distributions.

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*I spent long hours drilling mud cores in the postglacial deposits of the Esthwaite Water bogs and subjecting them to chemical analysis. Alas, I was less inspired by the chemistry of mud than by the remarkable diversity I found in the song dialects of the chaffinch in the surrounding valleys*

(Marler, 1985)

Following this observation of variation in the song of the chaffinch, *Fringilla coelebs*, Peter Marler, an ambivalent botanist, went on to perform his classic studies of song learning in the white-crowned sparrow, *Zonotrichia leucophrys*. Marler began by documenting that song in this species varies geographically (Marler & Tamura, 1962), and then performed experiments demonstrating that young males learn their song (Marler & Tamura, 1964). In the white-crowned sparrow and many other species (Mundinger, 1982;

Podos & Warren, 2007), geographical variants or 'dialects' result when males breed near where they learned their song(s), and the existence of geographical variation provides indirect evidence that song is learned (Kroodsma & Baylis, 1982). Imitation errors or improvisations can introduce novel songs or cultural mutants, which when imitated by other birds can produce geographical variation in song structure (Lemon, 1975; Lynch, 1996).

Behaviours acquired by social learning such as birdsong may provide messages concerning the identity, quality and motivation of the singer (Catchpole & Slater, 2008; McGregor, 1991). In several species of birds with a repertoire of two or more song types, song types with different messages or functions have different patterns of geographical variation (Beebe, 2002; Byers, 1996; Kroodsma, 1996; Soha, Poesel, Nelson, & Lohr, 2016), and vocalizations with similar functions share patterns of geographical variation (Baker, 2011). The inference from these results is that vocalizations with different spatial patterns of variation differ in their mode of vocal development, as has been found in two species, the chestnut-sided warbler, *Setophaga pensylvanica* (Byers & Kroodsma, 1992) and the grasshopper sparrow, *Ammodramus savannarum* (Soha, Lohr, & Gill, 2009).

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Most male white-crowned sparrows sing only a single song type (Baptista, 1975; Marler & Tamura, 1962), whereas most songbird species have repertoires of two or more song types (Read & Weary, 1992). In species with a single song type, different functions or messages may be relegated to different parts of the song (Marler, 1961; Nelson & Poesel, 2007; Osiejuk, Ratyńska, & Dale, 2007). Certain messages such as species identity or alerting would be best encoded in a relatively invariant acoustic structure within a species' song. Coding species identity requires an acoustic structure common to all members of the species (Marler, 1961). An alerting component should be structurally invariant so as to reduce a receiver's uncertainty of what to expect and thereby enhance detection success (Richards, 1981). In contrast, messages about motivation and individual or dialect identity necessarily require acoustic structures that vary between individuals or motivational states. Here I ask whether different parts or phrases in Puget Sound white-crowned sparrow (*Zonotrichia leucophrys pugetensis*) song that are inferred to have different functions exhibit different patterns of geographical variation.

All white-crowned sparrow songs begin with a whistle, followed by other phrase types (buzz, note complex, trill; Fig. 1). The whistle is a simple tonal phrase that has been hypothesized to serve as a species-identifying or alerting cue in song learning (Soha & Marler, 2000) or as an alerting component to adults that aids detection of message-bearing phrases that follow it (Shiovitz, 1975). An alerting as opposed to a species-identifying function for the whistle is supported by the observation that territorial adult males respond weakly to playback of isolated whistles, no differently from heterospecific song, while the local trill alone elicits strong territorial responses (Soha & Whaling, 2002). Two other phrase types, the note complex and trill, appear to encode different types of identifying and motivational information. The same note complex type is often shared between territory neighbours within a local population. Note complex sharing frequently comes about when yearling males overproduce two or more song types containing different note complexes when they arrive on territory and subsequently discard from their repertoire the type(s) not shared with territory neighbours (Nelson, 2000; Nelson & Poesel, 2009). Acoustic analysis and playback experiments suggest that the note complex encodes individual identity (Nelson & Poesel, 2007): note complexes differ more acoustically between individuals than do trills, and males respond stronger when a stranger's note complex is substituted for a neighbour's in a song than when a stranger's trill is substituted for a neighbour's trill. Also, the note complex is performed at a higher relative amplitude level when shared with a territory neighbour than when not shared (Poesel & Nelson, 2015), suggesting that the note complex functions in territorial interactions in addition to identifying individuals and local group membership. The structure of the trill varies geographically and has been used to define vocal dialects in this subspecies (Fig. 1; Baker, 1987; Baptista, 1977; Chilton & Lein, 1996; Nelson, Hallberg, & Soha, 2004). Playback of a foreign trill evokes weaker responses from territorial males than does playback of the local trill (Nelson & Soha, 2004). The trill may convey information about the singer's geographical origin, and variation in the length of the trill appears to signal aggressive intent (Nelson & Poesel, 2011). The function of the buzz phrase is unknown, and I do not consider it further.

Geographical variation in song over wide areas has been documented using subjectively defined syllable or song 'types' in the white-crowned sparrow and many other species (Catchpole & Slater, 2008; Mundinger, 1982; Podos & Warren, 2007). A common finding is that type sharing between two males decreases with increasing distance between them, as would be expected if the probability of dispersal decreases with distance. While

subjective categorization of audiospectrograms can provide high discriminability and repeatability (Jones, ten Cate, & Bijleveld, 2001), it cannot quantify acoustic dissimilarity within and among types, nor is it useful when types cannot be readily recognized. Here I also use quantitative measures of acoustic dissimilarity to address how the whistle, note complex and trill phrases vary among songs of the Puget Sound white-crowned sparrow recorded along a 560 km long linear transect of the Pacific northwest coast. If the whistle is an alerting or species-identifying component, I predicted that it would display little or no geographical variation in structure. On the other hand, if note complex and trill phrases convey identifying information at different spatial scales (neighbourhood and dialect), acoustic dissimilarity and geographical distance will be positively correlated. I also examined whether sharing of note complexes occurs on a more local scale than trills, as analysis in one local population found (Nelson & Poesel, 2009).

## METHODS

### Field Methods

The Puget Sound white-crowned sparrow is migratory. Males return from their wintering grounds in California to the breeding grounds in late March and April and sing frequently until pairs form in mid-April (Nelson & Poesel, 2011). I recorded a total of 512 males at 25 coastal sites from Smith River, California to Westport, Washington (Table 1, Fig. 1). Twelve of these sites had local populations of 30 or more males. To better achieve a uniform sampling of songs across the range, I chose a random subsample of 11–15 songs of high recording quality from each of these 12 sites, and combined these with all songs from the other 13 sites to yield a final sample of 267 songs. Crystallized adult song in this species is very stable (Baptista, 1975; Nelson & Poesel, 2007), so one exemplar is sufficient to represent each male's song type. I restricted my analyses to this section of the subspecies' range (which extends north into British Columbia) because my densest sampling was in this area and the sites formed a nearly linear sequence, which simplified analysis of the geographical range of song phrases. Heinemann (1981) and I have recorded males at several inland locations, and in all cases these males sang song types similar to those at the nearest coastal location. Smith River, California forms the southern border of trill dialect 11 (Fig. 1) and is near the southern border of *pugetensis*-like songs identified by Baker (1987). I encountered very different songs, similar to those recorded by Baker (1987) south of Smith River. At the northern end of the transect, Westport, Washington is near the southern border of trill dialect 5, which extends up to the Seattle, Washington area (Chilton & Lein, 1996; Nelson et al., 2004). I recorded 89% of the songs between April and June from 1998 through 2001. To fill gaps in the coverage, I added 29 males from three sites in 2004 (Cape Lookout), 2005 (Smith River) and 2013 (Pistol River). Two males at Smith River in 1999 and three males at Pistol River in 2000 and 2003 sang the same song types as were recorded later in the large samples, indicating that song does not change over a 6–10 year interval. Some males were banded as part of other studies; for the remaining birds I took care not to record the same individual twice by moving through the area and noting countersinging males. Songs were recorded with Sennheiser 'shotgun' microphone (MKH70) and a Sony TC-D10Pro digital tape recorder. A few males were recorded with a Sony TC-D5Pro II analogue cassette recorder. Many of my recordings are deposited in the Borror Laboratory of Bioacoustics, The Ohio State University ([blb.osu.edu/database/](http://blb.osu.edu/database/)). I geo-referenced each male's song perch using either a Magellan 315 GPS in the field or using Google Maps.

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