

## Cultural Evolution of Puget Sound White-Crowned Sparrow Song Dialects

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### Abstract

The songs of male Puget Sound white-crowned sparrows currently form about 12 dialects along the Pacific Northwest coast. In his survey of 1970, Baptista (*Condor* 1977; 79: 356–370) defined six of the dialects based on the song's terminal trill because most males at each locality shared the simple syllables (SSs) in this trill. The complex syllables (CSs) in the song's introduction varied among males at a locality, and were often shared among localities. From 1997 to 2004 we revisited nine of the sites Baptista studied to determine whether the SSs and CSs had changed over the 30-yr interval. Using Baptista's catalogs of SS and CS types as bases for comparison, we found that the relative proportions of CS types changed significantly more over time than did the proportions of SS types. These results suggest that SSs and CSs evolve independently. Observations were also made on the developmental mechanisms that either produce diversity or maintain uniformity in song phrases. In a survey of 670 field-recorded songs, unique improvisations occurred significantly more often in CSs than in SSs. In a laboratory experiment using hand-reared males and multiple song tutors, males were significantly more accurate in imitating SSs than CSs. In choosing their final song to keep from their overproduced repertoire, yearling males tended to retain the song type that matched the SSs in the song played back to them. We conclude by discussing how differences in the functions served by these two song phrases may have led to their different rates of cultural evolution.

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### Introduction

A major focus of research in evolutionary biology has been concerned with the causes and consequences of genetic and phenotypic variation within and between populations. Although the mode of inheritance differs between biological

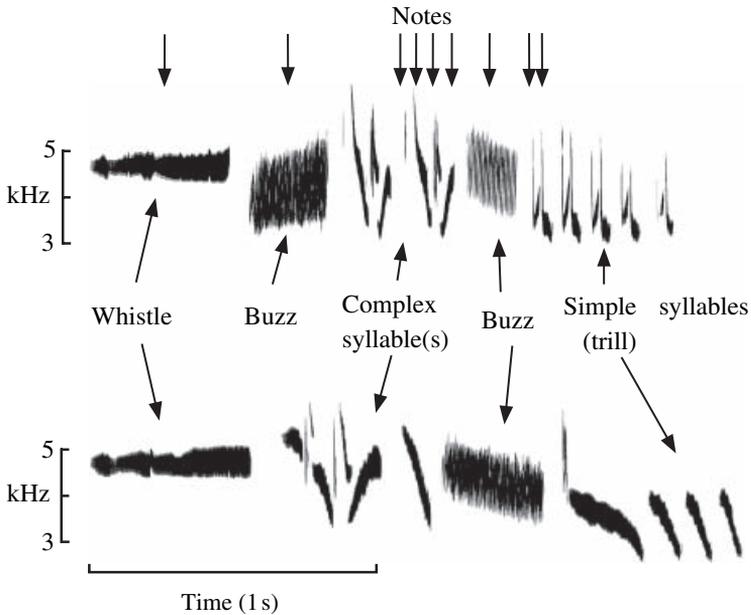
evolution (genetic transmission) and cultural evolution (learning), the same basic processes of mutation, selection, drift and immigration affect the course of evolution of both genes and cultural traits (Mundinger 1980; Cavalli-Sforza & Feldman 1981; Lynch 1996; Payne 1996).

Among cultural systems in animals, bird song dialects in temperate song birds are perhaps the most extensively studied. In song birds (Oscines), songs are learned by males, often early in life, typically from adult males. Transmission of songs between generations is usually horizontal or oblique instead of vertical, in contrast to genetic transmission (Baptista & Gaunt 1997). When song learning occurs near the site of breeding, local song dialects or neighborhoods often develop in which territory neighbors sing similar locally imitated songs (Lemon 1975; Krebs & Kroodsma 1980). There are now many studies documenting both stasis of dialects over decades (Thielcke 1987; Whitney & Miller 1987; Bradley 1994; Hansen 1999; Harbison et al. 1999), and rapid change (Payne 1985; Trainer 1989; Holland et al. 1996) in learned song traditions.

Several studies, adopting Dawkins' (1976) concept of the 'meme' as a unit of cultural inheritance, have examined factors influencing the transmission and success of memes in animal cultures. Of the processes affecting cultural evolution of song (Cavalli-Sforza & Feldman 1981), several studies have estimated mutation rates of memes (Slater et al. 1980; Lynch & Baker 1993; Lachlan & Slater 2003). Cultural mutations can be introduced into songs by two mechanisms: point mutations caused by copy error or improvisation, and recombination (Lynch et al. 1989). Bird songs often have an hierarchical structure, with notes grouped into syllables, syllables grouped into phrases, and phrases grouped into a song (Fig. 1), with the linear array of phrases being somewhat analogous to the sequence of genetic loci along a chromosome (Baker & Thompson 1985). In birds that learn two or more syllable or song types, novel memes can be created by combining elements from different syllables or songs (Lemon 1975; Slater & Ince 1979; Marler & Peters 1982b; Jenkins & Baker 1984). Other studies have documented the evolutionary processes of memetic drift in island populations of birds (Baker & Jenkins 1987; Baker 1996), and rates of meme flow between populations (Lynch 1996).

As yet, however, there appears to be little evidence of selection on alternative song memes or on different phrases (loci) within a song. Two studies have found a good fit of meme distributions to a neutral alleles model (Slater et al. 1980; Lynch et al. 1989). Payne et al. (1981) suggested that structural or functional constraints may limit the success of some cultural mutations within a song, but to our knowledge, no study of song evolution has examined this possibility.

There are several possible sources of selection on song, either ecologically, socially (culturally), or perceptually based. Among the latter are genetically based learning predispositions, which affect the acceptability of certain sounds as models for learning (Mundinger 1980). There is evidence that when given a choice, young male sparrows prefer to learn songs of their own species (Marler & Peters 1977) and even their own subspecies (Nelson 2000a). If certain song loci are particularly important cues to song recognition for example, then variability and



*Fig. 1.* Examples of Puget Sound white-crowned sparrow songs with terms used to describe song structure. The top song is a northern theme song from dialect 9 (Fig. 2), while the bottom song is a southern theme from dialect 1. The four phrase types (whistle, buzz, complex syllable(s), trill) are identified in each song. Most northern theme songs have a pair of complex syllables in between two buzzes, while southern theme songs have a single complex syllable preceding a single buzz. Notes, continuous tracings on an audiospectrogram, are marked with arrows above the northern theme

diversification at those loci might be constrained. Among possible influences on the evolution of memes are positive or negative frequency-dependent imitation of song types within a population (Whitney & Miller 1987; Gibbs 1990; Williams & Slater 1991) and learning strategies that maximize sharing song types with territory neighbors (Beecher et al. 1994; Ellers & Slabbekoorn 2003). Female preferences for certain song features that provide reliable information about male quality could also be a social influence on song evolution. Finally, ecologically based selection on sounds might be imposed by habitat-dependent effects on sound transmission (Slater 1989; Slabbekoorn & Smith 2002).

Our study has two parts. In the first, we describe changes in the songs of the Puget Sound white-crowned sparrow, *Zonotrichia leucophrys pugetensis*, over a 28-yr interval, with the intention of testing whether rates of cultural evolution are similar at two meme loci. At the end of the first part, and in a laboratory experiment comprising the second part, we examine several developmental processes that could produce the pattern of evolution observed in the field data. Song dialects have been extensively studied in this species (Marler & Tamura 1962; Baptista 1975; Baptista & King 1980; Baker & Thompson 1985; Chilton & Lein 1996), and our study takes as its starting point Baptista's (1977) original

description of six dialects in *Z. l. pugetensis* along the Pacific northwest coast of North America. Baptista described two main geographic patterns in song from his survey. First, the simple syllables (SSs) in the terminal trill of the song vary little among males at a given sampling location, while the complex syllables (CSs) in the song's introduction at the same location are usually more diverse (Fig. 1). Particular CSs also tend to be more widely distributed geographically than are SSs (Baptista 1977). Baptista defined the six dialects based on qualitative differences in the SSs, and the results of recent field playback experiments suggest that male *Z. l. pugetensis* are particularly attentive to the trill (Nelson & Soha 2004a).

In elaborating on Baptista's (1977) report that CSs were distributed in space independently of SSs, Heinemann (1981) proposed two mechanisms that might produce such a pattern. First, Heinemann (1981) suggested that hatching-year males might wander between several dialects, and that CSs may be learned at an older age than SSs. SSs might be more likely learned early in life in the natal dialect. Secondly, to explain the low variation in trill structure within localities, he reasoned from Marler & Peters' (1982a) description of overproduction and selective attrition of song, and hypothesized that the selective attrition process is primarily controlled by countersinging matching SSs with territory neighbors. If so, this could be a social/perceptual selective force producing relative stasis in SSs over time. We also use our field and laboratory data to test a third hypothesis concerning the production of cultural mutations in CSs and SSs. If CSs are more likely than SSs to mutate, either by learning errors or improvisation, then we would expect more rapid evolution of CSs in the absence of stabilizing selection.

## Field Observations

### Puget Sound White-Crowned Sparrow Song

All white-crowned sparrow songs begin with a whistle, followed by a variety of notes assembled into different phrase types (buzz, note complex, trill: Fig. 1). A note is defined as a continuous tracing on an audiospectrogram, separated from other tracings by at least 3 ms. Most adult males sing a single 'song type': a stereotyped sequence of song phrases. Baptista (1977) described two different 'themes' in *Z. l. pugetensis* songs based on the ordering of phrases within the song. Following the initial whistle, northern themes had a buzz, a pair of CSs, another buzz, and a trill of SSs. In southern themes, a single CS, buzz, and trill followed the whistle in that order. Syllables, categorized as CSs and SSs, have usually been used by researchers to define different geographic dialects in this species. In previous papers, we distinguished between a note complex, which is a sequence of unrepeated notes, and a syllable, a repeated or trilled sequence of notes. Note complexes are found in southern theme songs, while CSs are restricted to northern themes. For ease of comparison with previous work that did not distinguish between note complexes and CSs (Baptista 1977; Baker 1987; Chilton & Lein

1996), in this paper, we use ‘complex syllable’ to refer to both complex syllables and note complexes. In Baptista’s survey, Seaside, OR, separated the ranges of southern and northern themes. Subsequent work has uncovered two dialects of ‘northern’ theme songs several hundred kilometers south of Seaside (Baker 1987; Nelson 2000b).

### Field Methods

From 1997 to 2004 we recorded 670 song types from 652 males at 50 localities ( $n = 1\text{--}62$  song types per locality) throughout the range of the Puget Sound white-crowned sparrow from Trinidad, California north to Nanaimo, British Columbia. Fig. 2 shows the major recording localities visited between Apr. and June each year. Eighteen males sang two song types, most often early in the breeding season (Nelson 2000b). We used both song types from these males because the songs were stereotyped, and sung repeatedly and loudly. We did not include the songs of two males that were in ‘plastic song’, an intermediate stage of song development characterized by variable syllable structure and highly variable ordering of phrases within the song (Marler & Peters 1982b). Although several localities were visited in two or more years, we only included data from the year with the largest number of males recorded at each locality. We did not visit mainland British Columbia, which was thoroughly censused in 1993/1994 by Chilton & Lein (1996).

To examine the evolution of song phrases, we recorded 12–53 males at the nine localities (247 songs total) where Baptista (1977) recorded 10 or more males in 1970. We refer to this latter subset of cases as the diachronic sample, and for ease of exposition we will use 1998 as the average year in which these nine sites were sampled the second time. To increase sample size at three localities, we pooled recordings made from neighboring sites. Recordings made by Baptista and ourselves at Bandon Beach and Bullard’s Beach, OR (10 km apart), were pooled within years, as were recordings made at Ecola, Seaside and Gearhart, OR (along an 8-km stretch of coast), and Westport and Ocean City, WA (6 km apart). Based on Baptista’s (1977) published description of field sites and our knowledge of local conditions, we are confident that we recorded birds in the same locations that Baptista did at six of nine sample localities. The three possible exceptions were identified on Baptista’s original field tapes only by the nearest town. At two localities, ‘Newport’ and ‘Manzanita’, OR, we recorded birds in state parks bordering each town to the south. At ‘Friday Harbor’, WA (identified in Baptista 1977 as San Juan Island), our recordings were made at Friday Harbor Laboratories and Shaw Island, 2–5 km N and NE of Friday Harbor, although we made four recordings 10 km NW of Friday Harbor and found similar song types there. Given Baptista’s large sample size on San Juan Island ( $n = 62$ ), it seems likely that he recorded birds at a variety of sites there. With the possible exception of the Friday Harbor locality then, we do not feel it is likely that spatial differences in sampling confound our analysis of temporal changes in song.

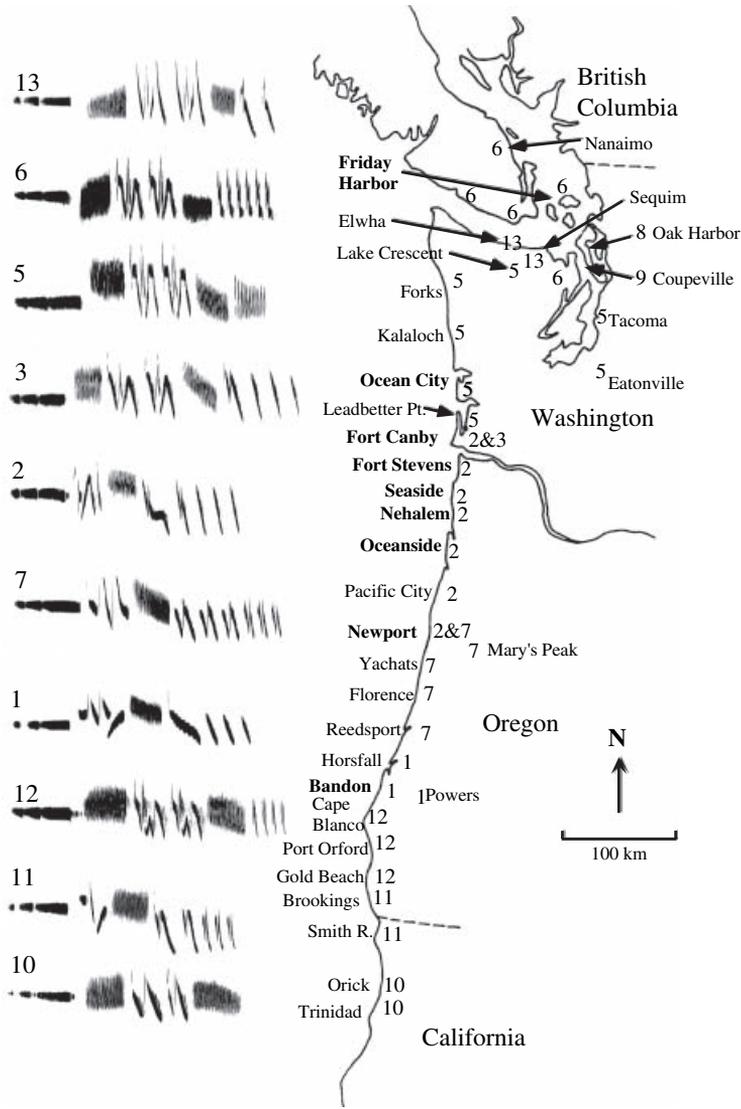


Fig. 2: Map of the northwest coast of North America showing 34 of our 50 sampling localities, and examples of the song dialects, identified by numerals, at each locality. The nine localities in our diachronic sample are marked in boldface. Dialects 8 and 9 occupy very restricted ranges in the Puget Sound area, and are illustrated in Chilton & Lein (1996)

**Recording and Song Analysis**

We recorded songs with a Sony TC-D10ProII digital tape recorder (Tokyo, Japan) and Sennheiser MKH70 ‘shotgun’ microphone (Wedemark, Germany).

Recordings of each song type from each male were digitized at 25 kHz with 16 bit amplitude resolution and saved as individual files using the Signal software program (Engineering Design 1999). We then prepared audio spectrograms (128 point FFT, time resolution = 5.1 ms) using a program written in Signal that normalized the grayscale and time and frequency axes. Most of our recordings are archived in the collection of the Borror Laboratory of Bioacoustics (<http://blb.biosci.ohio-state.edu>).

Baptista (1977) published catalogs of CS types (his Figs 4 and 6) and SS types (his Figs 3 and 5) that he encountered in his sample of songs. The figures in Baptista's paper portray three to six renditions of each syllable type, thereby enabling us to examine the range of variation he admitted within each syllable type. We reproduced these figures so that the time and frequency scales approximately matched those used in our audio spectrograms. Two judges (DAN and KIH) then independently sorted the CSs and SSs from the subset of 247 songs in our diachronic sample into Baptista's syllable type categories, and also, if necessary, into new categories. There were 250 CSs in the sample (three males sang two different CSs in their song), and 225 SSs (22 songs lacked the trill). We did not distinguish among the syllable subtypes Baptista named for several types. Judges erected new categories containing one or more syllables if they encountered syllables that did not appear to fit within the range of variation encompassed in Baptista's typology. DAN sorted the songs with knowledge of where the songs were recorded, and did so over the 8-yr period as recordings were made. KIH sorted sonagrams that were identified only by a four-digit label assigned by a random number generator, and did so over a period of several days. The sonagrams were shuffled before she received them, and she performed two sorts. First, the sonagrams were sorted on the basis of the CS into Baptista's categories (plus any new categories), and then they were sorted based on the SS. We compared our classifications to each other, and then tabulated the frequency of occurrence of each syllable type in our consensus classification at each locality to Baptista's published tables for 1970.

To measure the within-site diversity in syllable types, we calculated the Shannon diversity index,  $H$  (Magurran 1988):

$$H = - \sum_{i=1}^S x_i \ln x_i,$$

where  $x_i$  = the proportion of syllable type  $i$  out of a total of  $S$  types at locality  $x$ . We calculated  $H$  separately for CS and SS types at each locality for each time endpoint (1970 and 1998). To estimate the similarity in syllable type diversity between localities or between sample years we used the Morisita–Horn index (Horn 1966) as implemented in EstimateS (Colwell 1997):

$$C_{MH} = \frac{2 \sum_{i=1}^S x_i X_i}{\sum_{i=1}^S x_i^2 + \sum_{i=1}^S X_i^2},$$

where  $x_i$  = the proportion of syllable type  $i$  at locality and year  $x$ , and  $X_i$  = the proportion of syllable type  $i$  at another locality or year.  $C_{MH}$  was calculated separately for CS and SS types at each of the nine localities.  $C_{MH}$  ranges between 0 and 1 (perfect similarity). Of the many indices incorporating estimates of abundance that ecologists have devised to measure differences in species diversity (here syllable type diversity), the Morisita–Horn index appears to be the most robust to variation in sample size (Magurran 1988). Shannon diversities and Morisita–Horn indices were compared between CS and SS within sites using Wilcoxon matched-pairs signed ranks tests.

It is apparent from Fig. 2 that the sampling localities in our diachronic sample were not randomly distributed throughout the subspecies' range. Most localities were near the Oregon–Washington border, possibly because Baptista (1977) detected the transition from southern to northern themes in this area, and wanted to document this song change thoroughly. To examine possible spatial effects on song evolution, we used partial Mantel tests to correlate the matrix of  $C_{MH}$  calculated among all pairwise combinations of the nine localities in 1970 with the corresponding 1998  $C_{MH}$  matrix while controlling for geographic map distance between localities (Smouse et al. 1986). Tests were run for  $C_{MH}$  based on the frequency distributions of CSs and SSs separately.

We used the entire set of 670 songs to examine the occurrence of improvisation in CSs and SSs.  $N = 624$  for SSs because some songs were incomplete and lacked the trill. Our operational definition of an improvisation was a syllable or phrase that was a variant on one of the modal patterns or 'types' common in the subspecies (Figs 3 and 4), and that was unique, with three exceptions described below, to one locality. Examples will be illustrated in the Results section. If two or more males sang the same improvisation at one locality, irrespective of the distance between their territories (usually  $< 5$  km), we counted that as one improvisation 'event', on the assumption that one male likely was the source of the improvised syllable, and the other male(s) copied him. We also counted the number of males that sang each improvisation. We then tallied the numbers of independent improvisation events for CSs and SSs, and compared the proportions of improvised syllables using the method in Dixon & Massey (1969).

### Statistical Conventions

All tests in our study are two-tailed. In most cases we used non-parametric tests implemented in SPSS 11.5 and used tabulated exact probabilities when  $n < 20$  (Mundry & Fischer 1998). When using paired-comparison tests, we report  $n$  ( $n_{nt}$ ), where  $n_{nt}$  is the number of non-tied observations. To control the error rate in making related comparisons within a family of tests, we used the sequential Bonferroni procedure (Hochberg 1988). Mantel tests were run with the freeware program *zt*, with the original data matrices permuted 10 000 times ('raw matrix' option) (Bonnet & Van de Peer 2002).

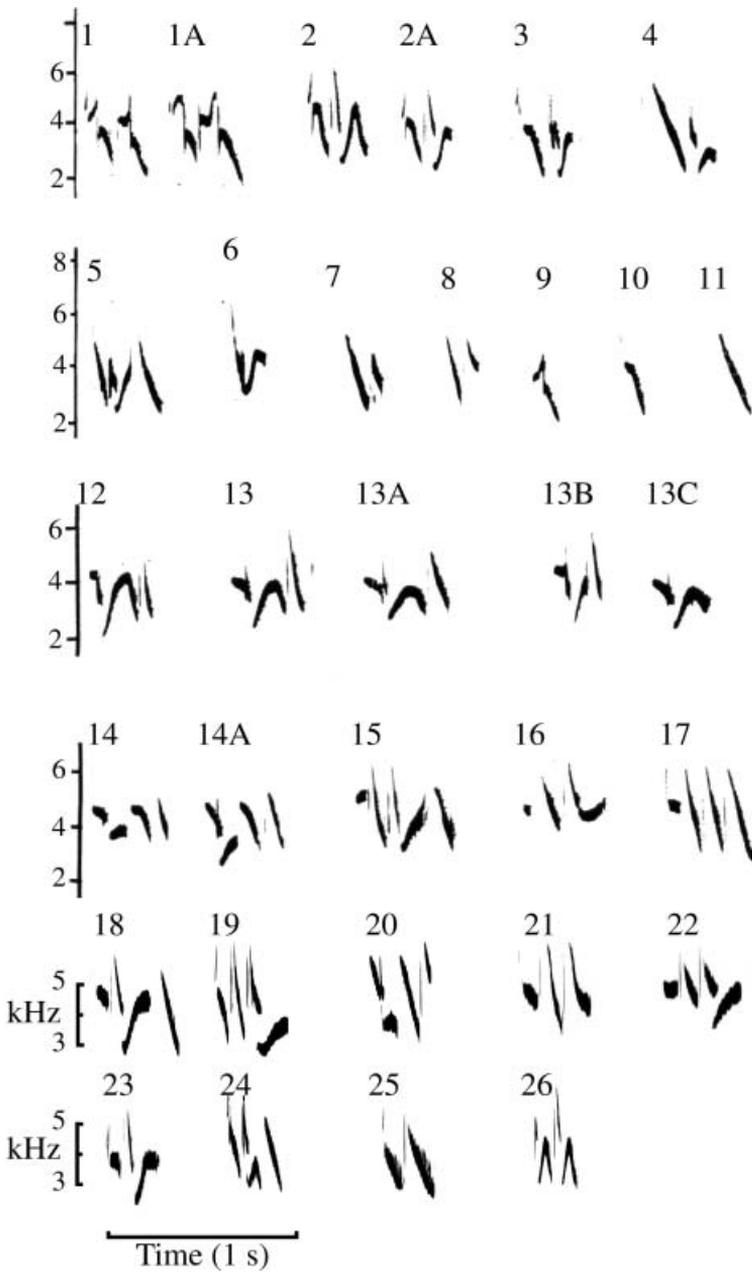
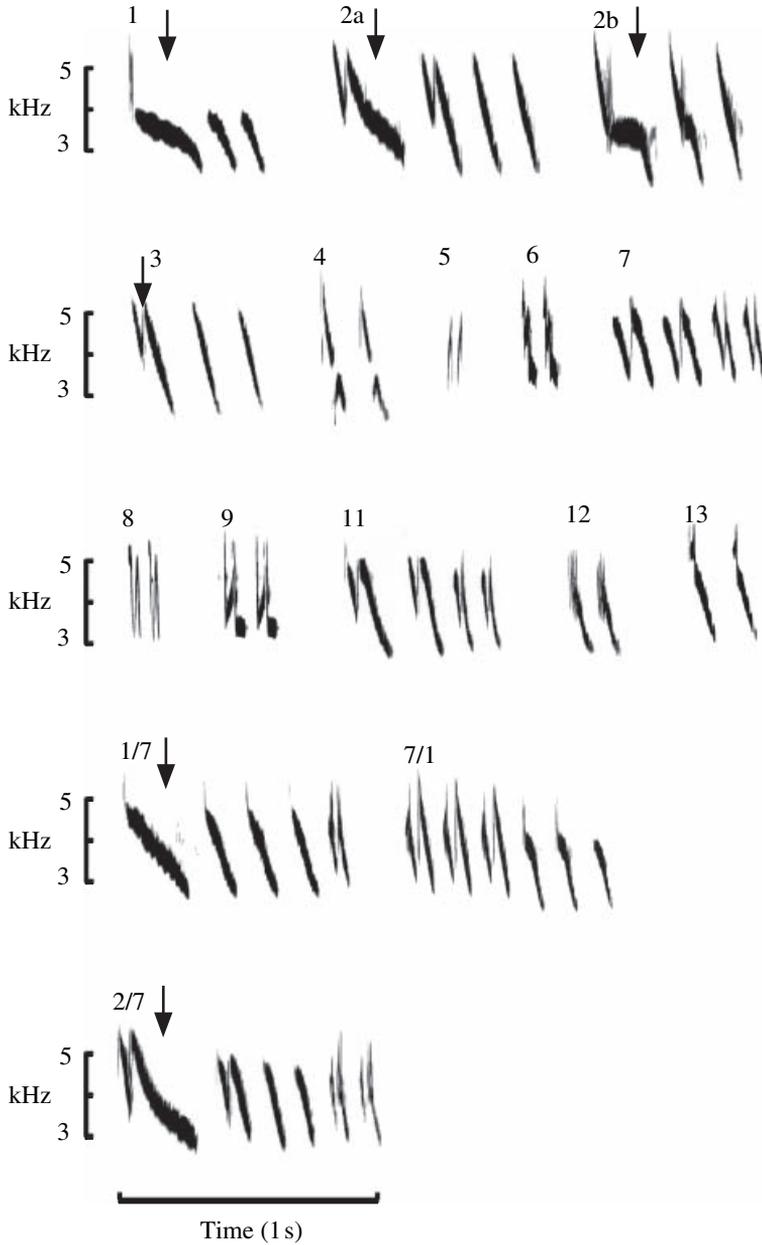


Fig. 3: Catalog of complex syllables (CSs). CS types 1–17 are reproduced with permission from Baptista (1977, Figs 4 and 6). CS types 18–26 are described for the first time in this study. CS types 1–11 and 24–26 are restricted to northern themes; the remainder occur in southern themes



*Fig. 4.* Catalog of simple syllable (SS) types (each syllable repeated twice) used to define local dialects (see text). Dialect 10 (Fig. 2) is unusual among white-crowned sparrow dialects in that the songs lack a terminal trill. Arrows point to note complexes at the beginning of some trills. Note complex 2a is more common in the south, and 2b to the north within the large dialect 2. At the bottom of the figure are shown three entire 'hybrid' trills commonly found at the southern and northern boundaries of dialect 7

## Results

### Inter-Observer Agreement in Categorizing Syllables

Of the 250 CSs in the 247 songs recorded from 1997 to 2004 in the diachronic sample, DAN placed 215 CSs into types 1–17 described by Baptista, while KIH placed 217 into these categories. Of these 217 or 215 CSs, the two judges placed eight CSs into different types (3.7% disagreement). Of the 33–35 CSs judged not to belong in existing categories by at least one judge, the judges independently agreed that 15 belonged in three new categories containing three, six, and six exemplars each (Fig. 3: types 18, 19 and 22). These were classified as three new CS types because, based on DAN's knowledge of songs in the entire sample, they were common at localities outside the diachronic sample. The remaining 18 CSs were classified as improvisations by consensus, although the judges initially disagreed on whether six of these were improvisations or belonged in types 1–17. There was similar agreement in classifying SSs into Baptista's categories as the two judges disagreed on only 11 of their assignments (5%). Because the categorization of syllables into types was highly repeatable among judges, we felt justified in basing the analysis of the remaining 420 songs in our entire data set on DAN's classification alone.

### Geographic Variation in Song

Figure 2 presents our current understanding of the distribution of song dialect areas in the Puget Sound white-crowned sparrow. Most of our recordings were made in coastal dune habitats. We recorded birds in forest clearcuts or towns at six inland locations (Powers and Mary's Peak, OR, and Forks, Elwha, Lake Crescent and Eatonville, WA, USA). Males at all six localities sang the same dialects that occurred at the nearest coastal locations.

Of the original six dialects described by Baptista in 1970, dialect 4, which occurred along a 45-km stretch of coast between Leadbetter Point and Ocean City, WA, appears to be extinct. We recorded one male singing dialect 4 10 km south of Leadbetter Point in 1997, but have not detected this dialect since then despite repeated work in the area. Since Baptista's original survey, seven more dialects have been described based on the structure of terminal trill outside of areas that Baptista visited. We confirmed the presence of dialect 7 (Heinemann 1981), dialects 8 and 9 (Chilton & Lein 1996), and dialects 10 and 12 (Baker 1987) where these authors originally described them. The dialect described by Baker (1987) at Harris Beach, OR (Brookings), has been replaced by dialect 11, which now stretches from Smith River, CA, to 6 km north of Brookings. A small dialect might still be present in between dialects 10 and 11 (Baker 1987), but we did not sample thoroughly in this area. We also found a new dialect, #13, between Sequim and Elwha, WA. Populations of the dialect areas likely range between about 100 (dialects 8 and 9) and thousands of males (dialects 1, 2 and 5).

Table 1: Occurrence of complex syllable types at nine localities sampled approx. 30 yr apart

Locality	Year	Complex syllable type																						Total
		1	2	3	4	5	6	12	13	14	15	16	17	18	19	21	22	Others <sup>a</sup>						
Friday Harbor	1970	4	11	26	12	7												5	65					
	2000		5	24	3	1													33					
Ocean City	1970	6	16			1													23					
	1999		17		1													1	19					
Fort Canby	1970	13					1												14					
	1998		34		1		19	1										8 <sup>b</sup>	63					
Fort Stevens	1970	15																	15					
	1998		2				21	1										3	27					
Seaside	1970	6			1		5	9	3										24					
	1998						11											1	12					
Manzanita	1970						8												8					
	1999						18	8										1	27					
Oceanside	1970						5	1	4										10					
	2004						13	2										1	16					
Newport	1970						1	7	4				2						14					
	1999						10	10										1	21					
Bandon	1970										13	3							16					
	1999										13			3	6	2	6	1	31					

<sup>a</sup>Category includes improvised songs.

<sup>b</sup>Includes one male with CS type 26.

### Cultural Evolution of Song

Figure 3 reproduces Baptista's original figures depicting the CS types in southern and northern theme songs, along with new syllable types encountered in our survey. We have continued Baptista's numbering system for identifying SS and CS types, adding numbers as necessary to accommodate new types. Because of large spatial gaps in Baptista's (1977) sample, we cannot be sure of how many of the novel CSs we encountered represent innovated CSs, and how many existed in 1970 at other localities that were not sampled. CS types 18 and 19 were common near Bandon, OR (and at other localities) in our sample but were not in Baptista's sample of 17 birds near Bandon (Table 1). The other new CS types we defined were found at locations other than those studied by Baptista. Because we sampled at many localities in addition to those visited by Baptista, we can be somewhat more certain of identifying cases of syllable extinction and can discriminate extinction from syllable 'emigration' from Baptista's nine localities. CS type 1, sung by 59 males throughout Washington state and northern Oregon in 1970, did not occur in our sample, nor in Chilton & Lein's (1996) sample. CS 14 also did not occur in our recordings of Oregon birds despite intensive sampling there. CS types 7–11 (each sung by one male in 1970) and type 16 (two males at Bandon in 1970) were not found by us. CS 17 (two males at Newport in 1970) was

sung by one male at Mary’s Peak, 50 km inland from Newport in 1999. Aside from CS 1 and CS14, the other CS types that were common in 1970 (2, 3, 4, 12, 13, and 15) were also common in our sample. Thus, most common CS types persisted over the 30-yr interval, and two common CS types went extinct along with several rare ‘types’ (which we would regard as improvisations in this study). Five of six SS types persisted over the same interval. Most (77%) of the 44 males in 1970 that sang SS type 4, now extinct, did not sing the now extinct CS types (1 or 14) in their songs (Table 2 and 3 in Baptista 1977). Therefore the extinction of these syllable types occurred independently of one another.

**Rates of Change of Syllable Occurrence**

We tabulated the frequency of occurrence of CS types (Table 1) and SS types (Table 2) at nine localities in both 1970 and 1998. Examples of changes in the occurrence of syllables at two localities are shown in Fig. 5. Comparison of Shannon diversity indices for CS and SS types within sites revealed that CS types were significantly more diverse than SS types both in 1970, as Baptista (1977) suggested [Fig. 6; Mann–Whitney U;  $T^+ = 0$ ,  $n = 9$  (7)], and in 1998 [ $T^+ = 5$ ,  $n = 9$ , Bonferroni  $p < 0.05$ ]. As measured by the Morisita–Horn index, the frequency distributions of CS types were less similar within the same site over time than were the distributions of SS types (Fig. 6;  $T^+ = 1$ ,  $n = 9$ ,  $p < 0.01$ ). As expected in a species with geographically variable song, the similarity in the

Table 2: Occurrence of simple syllable types at nine localities sampled approx. 30 yr apart

Locality	Year	1	2	3	4	5	6	7	Hybrid <sup>a</sup>	Other <sup>b</sup>	Total
Friday Harbor	1970						60				60
	2000						27				27
Ocean City	1970				2	22					24
	1999					13	1	1			15
Fort Canby	1970			14							14
	1998		21	21		3				6	51
Fort Stevens	1970			15							15
	1998		24	3							27
Seaside	1970		15	7							22
	1998		12								12
Manzanita	1970		11								11
	1999		27								27
Oceanside	1970		10								10
	2004		16								16
Newport	1970		14								14
	1999		10					1	10		21
Bandon	1970	15								1	16
	1999	26								3	29

<sup>a</sup>Hybrid refers to a trill of SS 7 followed by a trill of SS 2 (Fig. 4).

<sup>b</sup>Category includes improvised SSs.

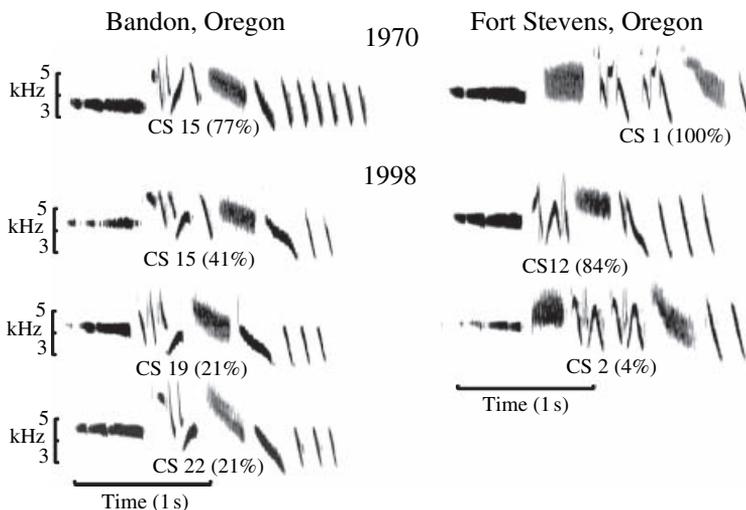


Fig. 5: Examples of change over time in songs at Bandon and Fort Stevens, OR. Recordings made in 1970 were provided by Luis Baptista. Thirteen of 16 males at Bandon sang CS 15 (shown); the other three sang songs containing CS 16, which is now extinct and has been replaced by four other CS types, the two most common of which are shown here (Table 1). At Fort Stevens in 1970, all males sang northern themes (dialect 3) containing CS 1. In 1998, 84% of 25 males sang southern themes (dialect 2) with CS type 12

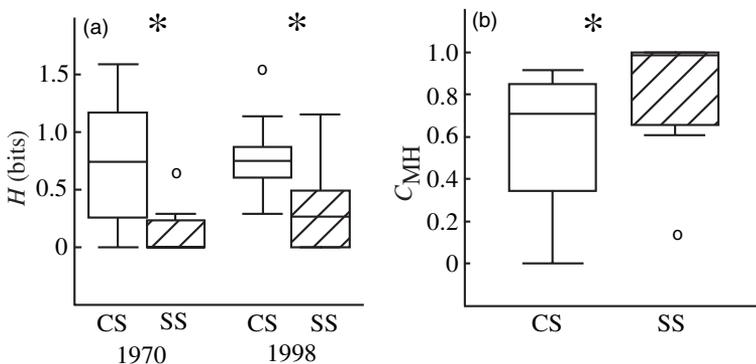


Fig. 6: (a) Within-locality diversity of complex (white boxes) and simple (hatched) syllable types expressed by the Shannon diversity index,  $H$ , in 1970 and 1998. (b) Similarity in the frequency of occurrence of syllable types within localities over a 28-yr interval. Similarity is represented by the Morisita–Horn index,  $C_{MH}$ . The lower and upper edges of the boxes represent the first and third quartiles; the median divides each box. The vertical lines (‘whiskers’) include the range of values within 1.5 times the inter-quartile range. Outliers are individual circles.  $n = 9$  for all groups,  $*p < 0.05$

frequency of occurrence of syllable types between localities was negatively correlated with map distance between localities for both CSs and SSs in both years (Table 3). When map distance between localities was controlled statistically,

Table 3: Mantel correlations between the Morisita–Horn index of similarity,  $C_{MH}$ , and map distance between localities for each year and phrase type, and partial Mantel correlations between  $C_{MH}$  between years holding map distance constant.  $C_{MH}$  ranges from 0 to 1

Variables	Mantel r
$C_{MH}(\text{CS } 1970)$ vs. map distance	−0.56*
$C_{MH}(\text{SS } 1970)$ vs. map distance	−0.50*
$C_{MH}(\text{CS } 1998)$ vs. map distance	−0.70*
$C_{MH}(\text{SS } 1998)$ vs. map distance	−0.69*
$C_{MH}(\text{CS } 1970)$ vs. $C_{MH}(\text{CS } 1998)$  map distance	0.24
$C_{MH}(\text{SS } 1970)$ vs. $C_{MH}(\text{SS } 1998)$  map distance	0.50*

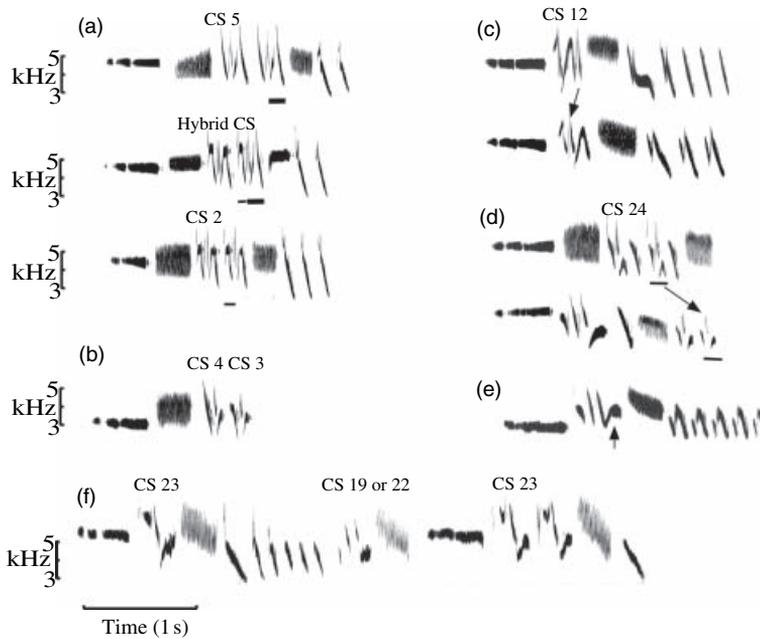
\*Family error rate for six comparisons controlled at  $p < 0.01$ .

the similarity in occurrence of CSs between localities in 1970 was not correlated with the same similarity measure in 1998, while the same test on SS similarity was significant (Table 3). These last two results indicate that when map distance between sample localities was controlled statistically, the distribution of CS types across localities was not predictable over time, while the distribution of SS types remained stable.

These field data describe the pattern of evolution in song: CSs are more variable within and between localities than are SSs and vary over time more than do SSs. This implies that the two syllable ‘loci’ are not tightly linked, and can recombine to form different combinations of syllable types. The results provide indirect support for Heinemann’s (1981) second hypothesis which predicts stasis in SSs over time within localities if males preferentially share SSs with their neighbors during matched countersinging. A more direct test will be provided below in the laboratory experiment. With a view to testing our third hypothesis, that CSs and SSs mutate at different rates, we next describe the production of cultural mutations in these two phrase types.

### Improvisation of CS and SS

In our sample of 670 songs recorded at all localities, we identified 30 cases of independently improvised CSs (4.5%), and 13 cases involving SSs (2.1%,  $n = 624$ ). These improvisation or cultural mutation rates for CSs and SSs differed significantly ( $Z = 2.40$ ,  $p < 0.02$ ). The improvisations occurred in 30 localities, apparently distributed uniformly within dialect areas. The mutation rate for SSs may be an overestimate. Two identical SS improvisations occurred at localities 20 km apart, hybrid trill 1/7 occurred twice 35 km apart, and hybrid trill 7/1 occurred twice 66 km apart (Fig. 4). To be conservative, we treated each occurrence as an independent event, but is possible that birds disperse over those distances from the site of learning. Only two males improvised both the CS and SS in their song. Three of the four main forms of improvisation of CSs are illustrated in Fig. 7: (i) borrowing notes from different syllables to create a new



*Fig. 7.* Examples of improvisation of complex syllables and simple trills recorded in the field. Syllable types are numbered corresponding to the catalogs in Figs 3 and 4. (a) Production of a 'hybrid' CS by borrowing parts, indicated by underlining, of two different common CS types. (b) A northern theme song with two different CS types, rather than one type repeated. (c) Rearranging the order of notes within a CS to produce a variant. The usual arrangement of notes within CS 12 is shown above. (d) Incorporating CS from a neighboring dialect into the trill. (e) The only possible example of elemental improvisation in the study, a unique note (above arrow) at the end of the complex syllable. The note appears to be derived from fusing the last two notes in the complex syllable directly above it. (f) One 'plastic song' sung by a yearling male molting into adult head plumage at Bandon, OR, on 24 Apr. 2003 (BLB catalog no. 28532). Note the extreme length of the song created by stringing together several songs or partial songs, the variable number of repetitions of CS type 23, and the single occurrence of CS type 19 or 22 in the middle of the utterance

'hybrid' syllable ( $n = 4$  events; Fig. 7a); (ii) using two different CS types in a northern theme song instead of repeating one type ( $n = 5$  events; Fig. 7b); (iii) singing a unique CS by deleting or rearranging notes from the common pattern ( $n = 13$  events; Fig. 7c); and (iv) consistently deleting or adding a CS repetition relative to the local norm (one repetition in southern themes, two repetitions in northern themes; Fig. 1) ( $n = 8$ ). Although individual males commonly varied the number of terminal SS repetitions from song to song, males rarely varied the number of repetitions of a CS across song renditions in crystallized song, although such variation was common during practice singing (plastic song; Fig. 7f).

The most common form of improvised trills existed at boundaries between two dialects where males sang hybrid trills containing a trill of one SS type followed by a trill of the other SS type (six events, Fig. 4). Two events consisted of

repeating the single long note at the beginning of the trill in some dialects (Fig. 4: dialects 1–3). As with CSs, males infrequently varied the number of repetitions of any note other than those at the song's end. In three events, males sang unique SSs, in one case incorporating the CS from a neighboring dialect into his trill (Fig. 7d). The improvisation depicted was also sung by one male at this locality in Baptista's sample (song H2 in Fig. 7 in Baptista 1977). Finally, two males added a buzz onto the end of their trill.

The cultural success of an improvisation was measured by the number of males that sang an improvised song. By definition, improvisations were rare within localities. Each of the 43 improvisation events was sung by a median of 1 male (range = 1–14). To accurately estimate the percentage of males at a locality that sang an improvised song we excluded events at sites where fewer than 20 males were recorded. There was no tendency for improvised SSs to be sung by a higher percentage of males within localities than were improvised CSs (Mann–Whitney U,  $n_{CS} = 24$ ,  $n_{SS} = 9$ ,  $Z = 0.81$ ,  $p > 0.05$ ). Each event was sung by a median of 4% of the males at a locality ( $n = 33$ , range = 2–61%). Three hybrid trills at boundaries between dialects 1, 2 and 7 were quite common (sung by 28, 34 and 61% of males: Fig. 4). The analogous form of improvisation occurred independently five times in CSs (Fig. 7b) but was only sung by one male at each locality (range = 3–5% of males within the locality).

To summarize, the field data indicate that improvisations (cultural mutations) were more likely to occur in CSs, but with the exception of common hybrid trills at two dialect boundaries, improvised CSs and improvised SSs were equally likely to be sung by other males. The production of novel improvised CSs may contribute to the rapid turnover in CS types over time described earlier.

### Laboratory Experiment

We performed a laboratory experiment using hand-reared males in order to examine the developmental mechanisms that might permit the independent evolution of CSs and SSs described above. Here we test Heinemann's (1981) two hypotheses described earlier: (i) SSs may be learned early in life in the natal dialect, while CSs may be learned later, and (ii) the selective attrition process is primarily controlled by countersinging matching SSs with territory neighbors. We also tested our third hypothesis: if CSs are more difficult to imitate and lead to mutations in CS structure (because they are acoustically more complex than SSs), then the pupils' imitations of tutor CSs should be less accurate than SS imitations.

### Methods

#### Subjects

We collected 13 nestling males (along with 15 females) from nine broods in late May 2000 in Robert Straub State Park, OR. Birds were 3–7 d old when collected. All of the adult males at Straub State Park sang dialect 2. Birds were

flown to the laboratory in Columbus, OH, within a few days of collecting. We hand-reared young birds using animal husbandry techniques described elsewhere (Nelson et al. 1995, 1996). We housed birds within 2 d of fledging singly or in pairs in sound isolation chambers. Pairs were formed opportunistically based on available chamber space, and contained same- or mixed-sex pairs as we could not sex birds in the first month. Birds typically alternated between being housed singly and in pairs within tutor blocks up until the time we first heard subsong (35 d of age on average), at which time males were housed singly for the remainder of the experiment. Most birds were housed singly for at least 2 d within each of the first four tutor blocks (see below). We sexed birds initially by listening for subsong, the first phase of vocal development in males, and verified sex the next spring when males had 5 to 7-mm-long cloacal protuberances, a testosterone-dependent character used to sex song birds. We maintained birds on the same photoperiod as in previous work: the ambient photoperiod for 38°N, advanced by 1 mo (Nelson et al. 1996).

### Early Tutoring

We used two different tutoring regimes, both of which males had learned from in earlier studies (Nelson et al. 1995, 1996). Regime A was designed to maximize precision in estimating the sensitive phase (for testing the first hypothesis), while regime B was designed to maximize opportunities for overproduction of song to provide subjects for testing hypothesis two (selective attrition of song). In regime A, seven of the 13 males were tutored with pairs of different songs in four successive 10-d-long blocks. The first block began 2, or rarely, 3 d after fledging (which occurred at 9–10 d of age) for each bird. Each block contained a pair of *Z. l. pugetensis* songs, chosen randomly from a menu of eight different dialects (not including the natal dialect). We chose acoustically distinct dialects so that identifying tutor imitations would be easy. To minimize pseudoreplication, we created 12 different sequences of tutor song pairs, with the different tutor songs counterbalanced with presentation order (block). No two males tutored with this regime were exposed to identical sequences of tutors. Regime B, applied to six males, resembled regime A in that a 10-d-long block of two *Z. l. pugetensis* dialects was begun 2–3 d after fledging. This block was then followed by a 40-d-long period in which four of the dialects not presented to a given bird in block 1 were played. Two of these six males heard the same pair of tutor songs in block 1, and the same four tutors in the second period. These two males did not learn from the same tutors. We also assume siblings to be independent replicates, because an analysis comparing song learning of males reveals that the songs developed by siblings in the laboratory are no more similar to each other than are the songs developed by randomly chosen unrelated males (D.A. Nelson & P. Marler, unpubl. data).

All males were tutored twice per day, morning and afternoon. In each 10-d-long block, one song type was repeated 180 times over 30 min, followed by 10 min of silence and then 180 repetitions of the other type. Tapes were played

every day, once at 08:00 h and once at 15:00 h. Thus, subjects heard each tutor type 360 times per day, and 3600 times total. Subjects heard each of the four tutors presented in the 40-d-long block 36 times per day, and 1440 times total. Songs were broadcast at approx. 74 dB in the center of the sound-attenuating chamber.

### **Song Recording and Analysis**

We recorded birds weekly beginning in the first week of Jan. using techniques described elsewhere (Nelson et al. 1995). We analyzed the recordings for evidence of imitations of tutor songs. We played tapes into a real-time spectrographic program (Engineering Design 1999), and saved sections containing singing into computer files. Each file, often containing dozens of consecutive songs from a single recording session, was printed as a continuous audiospectrogram using the 'Strip' command in Signal. We matched spectrograms of vocal material by eye to a catalog of spectrograms of the tutor songs (produced with the same aspect ratio in Strip). Identifications were made initially by one or two students and later confirmed by DAN. On each recording date, we counted the number of tutor songs represented, in whole or in part, in the bird's singing. For most birds, the number of tutor imitations produced peaked early in plastic song (see below). White-crowned sparrows sing with near-immediate variety in plastic song, i.e. they do not repeat a song type, or only repeat it 2–3 times before switching to a different one (Nelson et al. 1996). We generally examined 25–50 songs per bird from each day's recording.

We defined a song 'type' as a stable, repeated pattern that was sung over at least 2 wk. Song types usually became apparent in the first month of plastic song. Song types could be complete or partial imitations derived from one tutor song type, or 'hybrids', formed by combining phrases from two or more tutor song types. A song was considered crystallized when a male sang only one type that was repeated with little variation in note structure, especially the introductory whistle, which had to be produced with little random frequency modulation.

### **Sensitive Phase for Learning**

Based on weekly recordings throughout plastic song, we counted the total number of different tutors imitated and the number of phrases imitated from each (whistle, buzz, CS, SS) and determined the age at which each bird was exposed to each imitated tutor. We took the bird's age at the midpoint of the block to be the age of imitation. We used plastic song to estimate the sensitive phase as this provides a more comprehensive measure of what a bird has imitated than does the single crystallized song produced at the end of vocal development. For each male, we then calculated separately the mean age at which he imitated his CSs and SSs. We used Wilcoxon matched-pairs signed ranks tests to compare when CSs and SSs were learned ( $n = 12$  males; one male did not imitate and was excluded from all analyses of learning).

Because the tutoring period was relatively short in this experiment (40–50 d) it is possible that we may not have detected differences in when CSs and SSs were memorized. We therefore conducted a re-analysis of data on the timing of song memorization in two other subspecies of white-crowned sparrow. It is reasonable to extend the prediction to these two subspecies because CSs and SSs vary independently in space, as we have described in *Z. l. pugetensis*, in *Z. l. nuttalli* (Baker & Thompson 1985; Slabbekoorn et al. 2003), and to a lesser extent in *Z. l. oriantha* (Harbison et al. 1999). Eleven male Nuttall's white-crowned sparrows, *Z. l. nuttalli*, and 14 male mountain white-crowned sparrows, *Z. l. oriantha*, were tutored throughout the first year of life with pairs of tutor songs that changed every 10 d (Nelson et al. 1995). We calculated the mean age at which each syllable type was memorized, as described above.

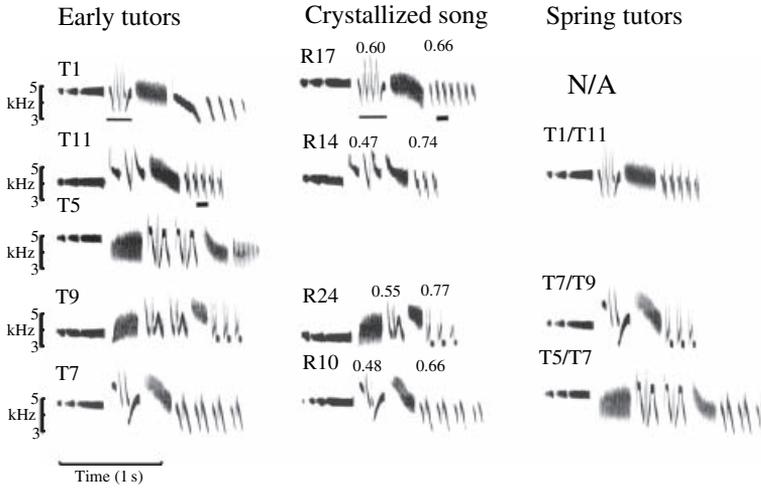
### Spring Tutoring

The second hypothesis, that males would selectively retain the dialect in their overproduced repertoire that matched the trill in the song played back to them, was tested with nine of 12 males. The three other males did not participate because they did not sing more than one complete tutor song. Spring tutoring began at approx. 210 d of age and initially stimulated singing and the song chorusing that occurs on the wintering grounds (DeWolfe & Baptista 1995). All males were tutored with a pair of white-crowned sparrow song types that were novel to them. We repeated each song on these tapes 72 times before changing to the second type after a pause of 40 s. After we were able to recognize multiple tutor imitations in each bird's plastic song, we switched to playback of a single computer-modified song type that was constructed by digitally splicing the introduction from one of the imitated tutors to the trill of another imitated tutor (Fig. 8). Which tutor song contributed the introduction was chosen by coin flip. Before switching to the synthetic tutor song, we waited until a male was singing imitations of two different tutor types at approximately equal frequencies (Nelson & Marler 1994). Most of the males infrequently sang complete or partial imitations of one to four other tutors. Matching playback began on 8 Jan. 2001 for the earliest bird and 8 Mar. for the latest. We played tapes twice daily, in the morning and afternoon, until the birds crystallized their final song. Birds heard 288 repetitions of the synthetic tutor each day.

Observed outcome frequencies (match CS, match SS, match both phrases, match neither) were compared with expected frequencies using a G-test with William's correction for small samples, which produces a more conservative test (Sokal & Rohlf 1981). Expected frequencies for the latter two outcome categories were estimated from the data, thereby decreasing the df by two.

### Imitation Accuracy

To address our third hypothesis, we used spectrogram cross-correlation to compare the accuracy of CS and SS imitations. We chose 10 song exemplars that



*Fig. 8:* Examples of imitation of tutor songs in the laboratory experiment. Tutors are shown in the left column; crystallized songs of the pupils are shown in the middle. Tutors are numbered after the dialect in which the songs were recorded (Fig. 2). Subject R17 created a hybrid imitation by combining parts from two different tutors (shown with different underlining). R14, R24 and R10 sang a complete imitation of one tutor song (T11, T9 and T7 respectively). Above each CS and SS in the four subjects' songs is the spectrogram cross-correlation value to the imitated syllable in the tutor's song to the left. In the right hand column are the hybrid spring tutor songs created by splicing together the introductory phrases from one imitated tutor to the terminal trill from another imitated tutor. Each subject (except for R17) sang complete imitations of both tutor songs while in plastic song

met our definition of crystallized song for each bird (see above). If possible, five non-consecutive song exemplars were sampled one day, and the other five 1 wk later. Songs were digitized as described above, and one CS and one SS from each were 'cut out' and saved in separate computer files. We also cut out one CS and one SS from each of the eight tutor songs. We then used spectrogram cross-correlation (Clark et al. 1987; Nelson et al. 1995) to estimate the accuracy of tutor imitation by cross-correlating all imitation files to all tutor files (within the same phrase type). Spectrograms were calculated with a 256-point FFT (10 ms resolution), time increment = 1.3 ms, and matrix amplitude normalization, and energy below 1500 Hz and above 9000 Hz was excluded from the cross-correlation. We calculated the mean cross-correlation value ( $n = 10$ ) for each CS and SS for each bird to all possible tutor CSs and SSs. The maximal mean cross-correlation was used to identify the putative tutor. Mean maximal values were compared within birds using a Wilcoxon matched-pairs signed-ranks test ( $n = 12$  males). It might be expected that cross-correlation values would be lower when comparing CSs than SSs simply because the former are longer and contain more notes ( $\bar{x} = 6$  notes,  $n = 8$  tutors) than the latter ( $\bar{x} = 2.5$  notes). If this were so, we would expect that the cross-correlations calculated between CS renditions by an individual would be lower than between SS renditions by the same individual. To check this possibility, the 10 crystallized CSs of each subject were

cross-correlated with each other ( $n = 45$  correlations possible among 10 objects), as were the 10 SSs. The mean within-bird cross-correlation value provides an upper bound on the estimated similarity value, and we tested whether within-bird CS cross-correlations were lower than within-bird SS values. We also compared the within-bird to the between-bird cross-correlations for each syllable type (calculated between tutor and pupil).

As a final check on the method, we calculated spectrogram cross-correlations between the CSs and SSs of all 12 wild males recorded at Florence, OR, that sang CS type 21 and SS type 7. We chose this sample because these two syllable types contain the median number of notes in CSs and SSs. In making this comparison, we assume that about half the males were yearlings (Nelson 2000b), who possibly learned from some of the adults the previous year. We estimate that we recorded about 80% of the males that sang along an 8-km stretch of road ( $n = 39$ ). For each of the 12 males, we took the maximal cross-correlation value between its CS and SS and the corresponding phrase in one of the other 11 males' songs as the between-bird correlation. We also calculated the mean within-bird cross-correlation for CSs and SSs, as described above for the laboratory-reared birds. This latter comparison was restricted to the 10 wild males that sang 3–10 times in our sample ( $\bar{x} = 5$  songs per male).

## Results

### Sensitive Phase

Twelve male *Z. l. pugetensis* imitated material, in whole or in part, from a median of three different tutor songs (range = 1–5). Examples of crystallized imitations are shown in Fig. 8. The median age of imitating all tutor material was 26 d (range = 15–40). However, there was no difference between the mean age at which each male imitated the two phrase types ( $T^+ = 9$ , ns, Fig. 9). No male imitated a novel tutor in the first spring.

We re-analyzed the timing of song memorization in *Z. l. nuttalli* and *Z. l. oriantha* that were tutored throughout the first year of life. Males of both subspecies learned CSs and SSs at the same age (Mann–Whitney U-tests; *nuttalli*:  $\bar{x} = 25$  d,  $U = 30$ ,  $n_{CS} = 10$ ,  $n_{SS} = 6$ ,  $p = 1.0$ ; *oriantha*:  $\bar{x} = 37$  d,  $U = 58$ ,  $n_{CS} = 13$ ,  $n_{SS} = 9$ ,  $p = 1.0$ ). We used U-tests with this data set, rather than matched-pairs tests because many males failed to imitate both a CS and a SS.

### Song Attrition

There were several possible outcomes to the experiment designed to influence the birds' choice of a crystallized song by playing back to them a 'hybrid' song consisting of the introduction of one of their imitated tutors and the trill of a second tutor. Heinemann (1981) had hypothesized that the more localized geographic distribution of SSs could be produced by preferential retention of the song type containing matching SS during countersinging interactions between males.

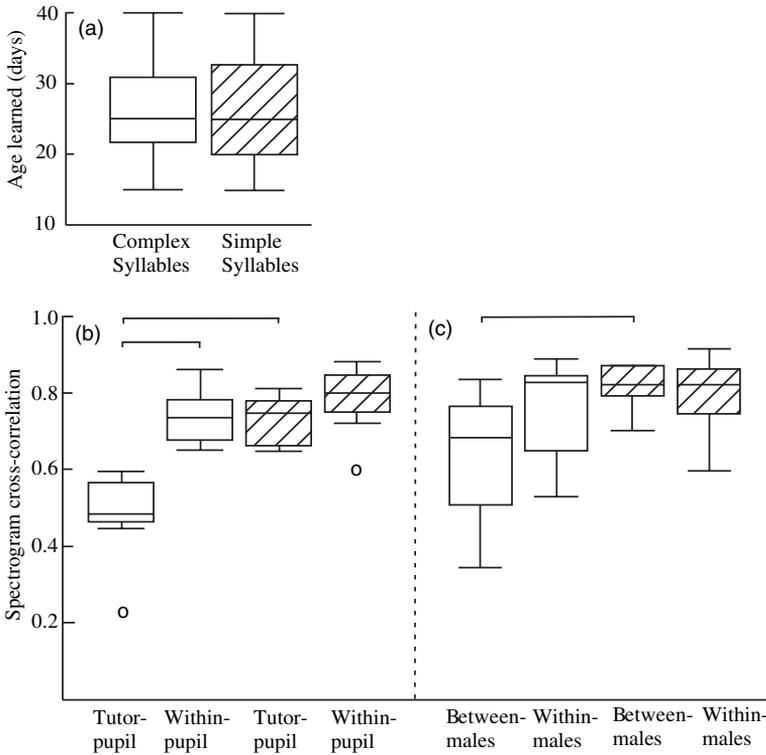


Fig. 9: Results of the song learning experiment using hand-reared male *Z. l. pugetensis*,  $n = 12$  in panels (a) and (b). (a) Males learned CSs and SSs at the same median age. (b) The boxes present statistics for comparisons between 10 renditions of each pupil's syllables and the single tutor syllable that yielded the maximal mean cross-correlation to the pupil's syllable (tutor-pupil), and the average of all possible comparisons between the 10 renditions of each pupil's crystallized CS and SS (within-pupil). (c) Between- and within-male comparisons for 12 wild males at Florence, OR, that sang the same song type.  $n = 10$  for within-male comparisons. The spectrogram cross-correlation ranges from 0 to 1. Horizontal bars connect significantly different paired comparisons (Bonferroni  $p < 0.05$ )

Alternatively, males could create a hybrid crystallized song themselves by recombination, matching both phrases. In support of Heinemann's hypothesis, six of nine males crystallized the song type that matched the spring tutor song's SSs, two matched the introduction, and one male did not match either phrase and crystallized one of his other imitations (Fig. 8). None created a hybrid song that matched the spring tutor (see below). The preference for matching the spring tutor's SSs was not significant (Likelihood ratio test,  $G_{adj} = 2.33$ ,  $df = 1$ ,  $p = 0.15$ ).

**Imitation Accuracy**

The 12 males tutored with regime A or B in 2000 that imitated a tutor reproduced SSs more accurately than CSs ( $T^+ = 0$ ,  $n = 12$ ,  $p < 0.05$  for family

of four comparisons, Fig. 9b). Using the maximal spectrogram cross-correlation coefficient to identify tutors revealed that 11 males learned both the CS and SS in their crystallized song from the same tutor, while one male (R17 in Fig. 8) created a hybrid crystallized song by combining the CS from one tutor with the SS from another tutor. His hybrid song was not produced in response to a hybrid spring tutor: he did not participate in the song attrition experiment because he rarely sang a complete version of one of his two imitations. In each case, the tutor identified by spectrogram cross-correlation agreed with our subjective visual identification. There was no evidence that the spectrogram cross-correlation technique was biased to provide lower values for comparisons involving CSs than for SSs. The mean within-bird CS cross-correlation did not differ significantly from the mean within-bird SS cross-correlation (Wilcoxon matched pairs test,  $T^+ = 17$ ,  $n = 12$ ,  $p > 0.05$ , Fig. 9b). The mean within-bird cross-correlation was significantly higher than the between-bird cross-correlation for CSs ( $T^+ = 0$ ,  $n = 12$ ,  $p < 0.05$ ), but not for SSs ( $T^+ = 21$ ,  $n = 12$ ,  $p > 0.05$ ).

The analysis of songs of wild males at Florence yielded similar results. Cross-correlations between the CSs of 12 males that sang CS type 21 were significantly lower than were the correlations between their renditions of SS type 7 (Fig. 9c: Wilcoxon matched pairs test,  $T^+ = 3$ ,  $n = 12$ ,  $p < 0.01$ ). Correlations calculated within males did not differ between the phrase types of wild males ( $T^+ = 21.5$ ,  $n = 10$ ,  $p > 0.05$ ). In contrast to the hand-reared birds, the mean within-male cross-correlations did not differ from the between-male cross-correlation for either phrase type in the wild males. Taken together, the results imply that renditions of the same CS type sung by different birds are less similar to one another than are renditions of the same SS type.

To summarize the laboratory experiment, we found no evidence to support Heinemann's (1981) first hypothesis, as males imitated CSs and SSs at the same ages. As predicted by Heinemann's second hypothesis, in choosing a song type from their overproduced repertoire to retain as their single, adult song, males tended to choose the song type that matched the SSs in the tutor song played back to them in the spring, although the effect was insignificant. Finally, males' imitations of tutor CSs were significantly less accurate than were SS imitations.

## Discussion

A major conclusion that emerges from our comparison of Puget Sound white-crowned sparrow songs recorded over a 28-yr-long interval is that the majority of the complex and SS types that make up a song have persisted over that interval. What has changed is the relative frequencies of CS types within songs at localities. To use the meme terminology, if the syllable types are 'alleles' at different syllabic 'loci' (CSs in the introduction and SSs in the trill), the loci have recombined independently over time to produce some novel combinations of alleles and have changed the relative frequencies of other combinations. It is a common finding from other studies of long-term change in bird song that lower-order units (notes and syllables) are more stable than are higher-order units

(syllables, phrases and songs) [saddleback, *Philesturnus carunculatus* (Jenkins 1977); chaffinch, *Fringilla coelebs* (Slater & Ince 1979; Lynch et al. 1989); indigo bunting, *Passerina cyanea* (Payne et al. 1981); savannah sparrow, *Passerculus sandwichensis* (Bradley 1994; Burnell 1998); Nuttall's white-crowned sparrow, *Zonotrichia leucophrys nuttalli* (Slabbekoorn et al. 2003)].

Our study focused on changes in the structure and frequency of occurrence of syllable types within and between localities. We did not undertake a formal analysis of note structure here, but the fact that so many syllable types described in 1970 by Baptista (1977) still exist suggests that the basic structure of most component notes has not changed much either. As described below, most new syllable types seem to be created when males rearrange the order in which a limited repertoire of note types occur within a syllable. The only possible example in this study of an improvised note occurred in one song recorded at Yachats, OR, where two notes were possibly 'fused' sequentially to form one note (Fig. 7e). In this study, almost all improvisation events were combinatorial in nature, in which notes are rearranged, inserted or deleted to create novel syllables (Fig. 7a–d). These forms of improvisation correspond closely to those described in other bird species (Jenkins 1977; Slater & Ince 1979). Several pairs of syllable types contain very similar syllables, and one member of the pair may have been derived from the other by rearrangement of notes (cf. types 2 and 12 in Fig. 3), or addition/deletion of a note (types 18 and 23, 3 and 24, 15 and 22). Presumably, an improvisation appearing in a small population could be copied and increase in frequency over time until we would recognize it as a common syllable 'type'.

Stochastic factors are probably responsible for the apparent loss of rare syllable types over time. Most of the apparently rare syllable types in 1970 did not occur in 1999 probably because they were unlikely to be copied by young males. An exception is the improvised song at Bandon (Fig. 7d), which in 2003 was sung by four males. However, some very common types (CSs 1 and 14, SS 4) were also lost over time, and it seems probable that factors other than sampling effects must be responsible for these losses.

Our field recordings reveal that males are significantly more likely to improvise CSs than SSs. Baker & Thompson (1985) also identified a greater number of rare, presumably improvised, CS types than rare SS types in their detailed analysis of six dialects of *Z. l. nuttalli*. The results of our laboratory tutoring experiment indicate that CS imitations are less accurate than are SS imitations. The comparisons involving wild males at Florence that all sang the same CS and SS types closely paralleled those derived from our tutoring experiment. These males were recorded within 8 km of one another, and some may have been tutored by other males in the sample. The tutor-pupil difference in CS structure could reflect active improvisation on the pupil's part, or difficulty in imitating the more complicated acoustic structure of CSs. Either process would have the effect of introducing and maintaining greater variation in the CS phrase.

Meme flow, the movement of syllable types into or out of an area driven by dispersal of males from the site of song memorization could be sufficient to produce the significant change in distribution of CS types over time, and would be

consistent with the failure to document concordance between song dialects and genetic structure in this subspecies (Soha et al. 2004). However, dispersal alone cannot explain both the change in CS frequencies and the stability in SS frequencies because the two meme loci evolve independently when all localities are considered. The distributions of CSs and SSs must be controlled by separate factors.

Several forces of selection, either perceptual or social, might influence the cultural success of songs or syllables, and there are indications that these forces act differently on CSs and SSs. First, we did not find any evidence in *Z. l. pugetensis* to support Heinemann's (1981) hypothesis that the sensitive phases for memorizing CSs and SSs differ, but this result must be qualified by the relatively short duration of tutoring used in this experiment (40–50 d). A re-analysis of data obtained when Nuttall's and mountain white-crowned sparrows were tutored throughout the first year of life also failed to demonstrate a difference in when syllable types were memorized. It is possible though that a different experimental tutoring regime would yield different results.

Secondly, differences in when CSs and SSs are influenced by environmental input could be manifest not during song memorization, but during territory establishment as proposed in Heinemann's (1981) second hypothesis. Even if males learn their CSs and SSs at the same time on average, if matched countersinging during territory establishment is guided preferentially by the SSs, this would produce stabilizing social selection on SSs, while leaving CSs relatively free to vary within localities. The results of our laboratory test, although non-significant, are consistent with the interpretation that males pay particular attention to variation in the SS at this stage. In choosing a song for crystallization from their overproduced repertoire of plastic songs, males tended to choose the imitated song type that matched the SS of the song played back to them (Fig. 8).

Both of the developmental processes we documented – the tendencies to improvise more CSs, and to imitate them less accurately than SSs – will have the effect of introducing and maintaining a higher degree of within-population variance in CSs than in SSs. Before we can conclude that these processes are evolved mechanisms (*sensu* Williams 1966) that produce inter-individual variation in CS structure, we will require information on what functions these song phrases serve.

There is a variety of evidence indicating in this and other species that males and females perceive song variation differently (Baker et al. 1987; Thompson & Baker 1993; Ratcliffe & Otter 1996). Elsewhere we present evidence that male *Z. l. pugetensis* are especially attentive to variation in SSs (Nelson & Soha 2004a,b). One possible functional interpretation is that sharing the SSs with neighbors is important in mediating male–male competitive interactions (Nelson & Soha 2004a). A preference for sharing SSs with neighbors could produce the uniformity of SS types (lower *H*) within localities, although the mechanism(s) by which males benefit from sharing songs, or parts thereof, with neighbors is still unclear (Beecher et al. 1997).

Several factors acting on individual singers might have the effect of maintaining diversity in CS types within localities. Particular CS types may be functionally neutral, but selection may have favored improvisation at this song locus if distinctive CSs facilitate individual recognition (Slater 1989; Searcy & Nowicki 1999). Another possibility is that females have a mating preference for song complexity (Searcy & Nowicki 2000), expressed in this subspecies in the CSs. Identifying the functional roles these syllable phrases play in communication remains a problem for the future.

### Acknowledgements

We thank Pam Wenzel for help with the field work, and Kacey Franz for help in the lab. Jack Dumbacher and Doug Long at the California Academy of Sciences loaned us Baptista's original field tapes. The manuscript was improved by the comments of three reviewers. Supported by IBN-9513821 and IBN-9816651 to DAN. We are grateful to the States of Oregon and Washington, their State Parks Departments, the Oregon Dunes National Recreation Area, the University of Washington, and the city of Port Orford, OR, for permission to work on their properties. Birds were recorded and collected under the authority of federal, state, and local permits, and research was approved by the Ohio State University ILACUC Protocols 95A0007 and 00A0005.

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*Received: March 15, 2004*

*Initial acceptance: May 18, 2004*

*Final acceptance: July 14, 2004 (S. K. Sakaluk)*