

LONG-TERM CHANGES IN SONGS AND SONG DIALECT BOUNDARIES OF PUGET SOUND WHITE-CROWNED SPARROWS¹

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Abstract. Few studies have examined song variation in populations of birds over sufficiently long periods of time to demonstrate changes in the geographic distribution of song types. Baptista (1977) recorded songs of Puget Sound White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*) over much of their range in 1970 and 1977, describing six song dialects on the basis of differences in the terminal trills of songs. We documented the distribution of song dialects in the northern part of the range of this subspecies in 1993 and 1994. The two most-widespread dialects have persisted, but the limits of their distributions have changed. One dialect with limited distribution in 1970 was not encountered. We describe two previously undocumented dialects with limited distribution, and identify sub-dialects whose distribution seems to be related to barriers to dispersal. We have no reason to believe that changes observed are the result of selection for one song type over another.

Key words: cultural transmission; dialect boundaries; song dialects; White-crowned Sparrow; *Zonotrichia leucophrys pugetensis*.

INTRODUCTION

In all species of oscine songbirds studied to date, young birds learn species-typical songs from older conspecifics (Slater 1989, Catchpole and Slater 1995). In many species, learning is restricted to a brief sensitive period early in life. Errors in song learning, combined with fidelity to the natal area, are thought to give rise to the geographic variation noted in the songs of most species. When these song variants show a mosaic distribution, separated by fairly sharp boundaries, they are described as song "dialects" (Thielcke 1969, Baker 1987).

For most species, little is known about the lifespan of local song variants, even whether particular song types persist longer than individuals (Payne et al. 1981). In some species, song types arise and disappear rapidly. The colony-specific songs of caciques (*Cacicus cela*) sometimes change within a single breeding season (Trainer 1989). In contrast, specific song types of other species are remarkably resistant to change. Of 25 Wood Thrush (*Hylocichla mustelina*) song types recorded in New York in 1981, 23 were also recorded in 1990 (Whitney 1992). Song dialects of Rufous-collared Sparrows (*Zonotrichia capensis*)

in Argentina have persisted for at least 20 years (Handford 1981, 1988). The song types of Chaffinches (*Fringilla coelebs*) have an intermediate degree of persistence; eight of 23 song types recorded in 1960 were still present in 1978 (Ince et al. 1980).

The White-crowned Sparrow (*Zonotrichia leucophrys*) is probably the best-studied species with regard to song. Most males sing a single, simple song type, which is remarkably stable over the life of the individual (Petrinovich 1988). Variation in song between populations is generally much larger than the variation within a population (Thompson and Baker 1993), and these geographic differences are described as song dialects.

In White-crowned Sparrows, dialect populations are often separated by fairly sharp boundaries, which do not appear to coincide with changes in habitat (Baptista 1977). Long-term survival of specific song dialects permits investigation of the permanence of boundaries between them. Trainer (1983) showed that a boundary between White-crowned Sparrow dialects remained virtually stationary over a period of ten years. However, it is hard to imagine why the limits of distribution of a dialect would not move over time in response to population events that are not related to song variation per se (Slater 1989), such as the occupation of newly-created habitat (see Discussion).

¹ Received 26 October 1995. Accepted 19 March 1996.

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In 1970, Baptista recorded the songs of male Puget Sound White-crowned Sparrows (*Z. l. pugensis*) over much of their range in British Columbia, Washington, and Oregon (Baptista 1977). He distinguished six variants on the basis of the terminal trills of songs. Having found little geographic overlap in trill types, he described songs with specific trills as song dialects. He grouped these dialects into two broader "themes" on the basis of the song's syntax.

In 1977, Baptista and D. Martin extended this survey to include portions of the Olympic Peninsula not covered by the 1970 survey. Some of their findings are reported in Heinemann (1981) and DeWolfe and Baptista (1995). These latter observations confirmed the discrete geographic distribution of song dialects in this region. Heinemann (1981) documented a seventh song dialect in Oregon in 1977-1978.

These surveys provided an opportunity to examine the changes in song dialect distribution over a longer period and over a greater geographic range than had been attempted in previous studies. In 1993 and 1994, we recorded the songs of male White-crowned Sparrows in regions denoted as dialects 4, 5, and 6 in the northern part of Baptista and Martin's 1970 and 1977 surveys. Specifically, we set out to determine whether the song dialects recorded by Baptista and Martin have survived a quarter-century of cultural transmission and, if so, whether the boundaries between those dialects have remained stationary. We also considered the possibility that new dialects have arisen since the earlier survey. Further, we looked for evidence of a relationship between the distribution of songs types and barriers to dispersal of individuals.

To avoid possible confusion between previous studies, throughout this manuscript we refer to the results of Baptista's 1970 survey of White-crowned Sparrow songs, reported in his 1977 manuscript as "Baptista 1977." We refer to results of the follow-up survey conducted in 1977 by Baptista and Martin, which have not been published formally, as "Baptista and Martin unpubl. data."

METHODS

Songs of male Puget Sound White-crowned Sparrows were recorded in 46 localities in British Columbia (BC) and Washington (WA) between 5 and 18 May, 1993, and between 24 April and 20 May, and on 28 June, 1994 (Fig. 1). The

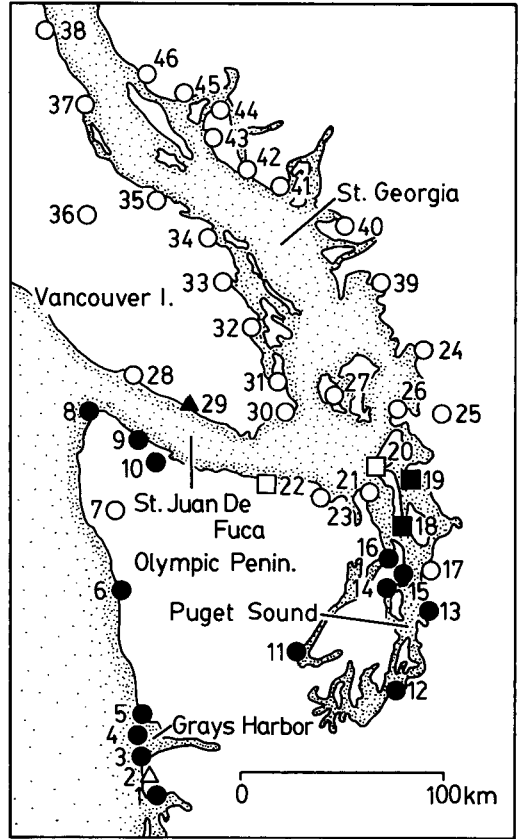


FIGURE 1. Map of localities sampled. Locality numbers correspond to Tables 1, 2, 3, and 4 and to notations in text. Symbols represent the most common terminal trill type in each locality: open triangle = trill type 2; closed circle = trill type 5; open circle = trill type 6; closed square = trill type 7; open square = more than one trill type was common; closed triangle = no terminal trills were recorded.

survey was meant to include birds in regions denoted as dialects 4, 5, and 6 by Baptista (1977).

In the breeding season, Puget Sound White-crowned Sparrows are rarely found more than 20 km from the sea (Chilton et al. 1995). Within that band, they are common throughout the survey area. They are particularly abundant in city parks and gardens, in forest clearings, and along coastal sand dunes (Baptista 1977). Wherever possible, we recorded birds in the same localities as those described in Baptista (1977) and Heinemann (1981). The distribution of these localities reflects, in part, regions of particularly high abundance.

To achieve our objective of searching for a

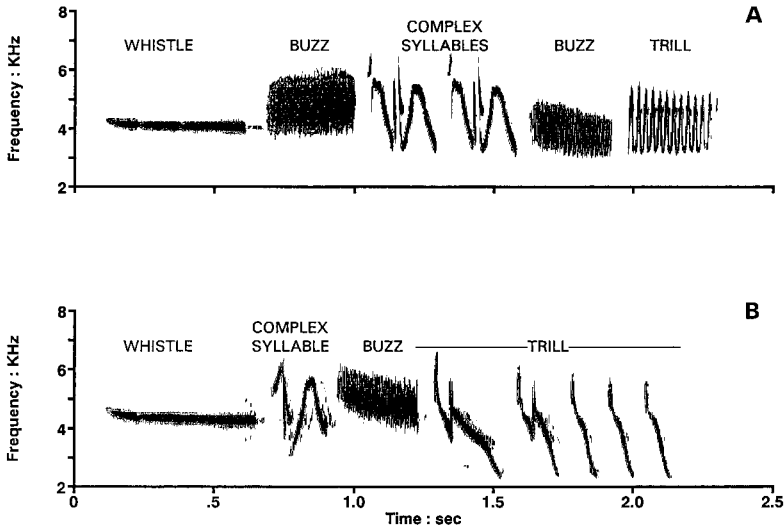


FIGURE 2. Syntax of northern theme (A) and southern theme (B) songs, illustrating terminology used.

relationship between the distribution of song types and barriers to dispersal of individuals, we recorded birds along both sides of the Strait of Georgia north to Campbell River (locality no. 38 in Fig. 1) and Powell River (loc. 46), and on both sides of the Strait of Juan De Fuca west to Neah Bay (loc. 8) and Port Renfrew (loc. 28). Some of these regions were not visited by Baptista (1977) or Baptista and Martin (unpubl. data).

All localities mentioned in this publication can be found on BC provincial or WA state highway maps. Even so, some clarification of localities is necessary. "Cleveland Dam" and "Stanley Park" (Baptista 1977) are sites a short distance apart in greater Vancouver, BC, and along with the community of Horseshoe Bay, are reported here as "Vancouver" (loc. 40). "Butchard Gardens" (sic) (Baptista 1977) is a commercial enterprise in Central Saanich (loc. 31). "Junction Highway 4" (Baptista 1977) is the junction of highways 4 and 19 on Vancouver Island, near the community of Parksville (loc. 35).

Songs were recorded on Sony HF and HF-S cassette tapes with a Sony TCM-5000EV tape recorder and a Gibson P-650 parabolic microphone or a Tandberg TM6 microphone and 46 cm parabolic reflector. Spectrograms of all songs of each male were viewed using RTS (Real Time Spectrogram) program, and hard copies of representative spectrograms were generated with SIGNAL (Sound Analysis System) program (Engineering Design, Belmont, MA).

RESULTS

We recorded 3,200 songs from 276 male Puget Sound White-crowned Sparrows. One of these individuals sang three song types, and 24 others sang two song types, for a total of 302 different songs. Details of the songs of males singing more than one song type are considered in more detail elsewhere (Chilton and Lein 1996).

All but four males produced songs whose syntax of introductory whistle (W), buzzes (B), complex syllables (CS), and terminal trill (SS) match Baptista's description of the "northern theme" (W-B-CS-CS-B-SS) (Fig. 2A). Two males produced songs whose syntax closely resembled dialect 2 from Baptista's "southern theme" (W-CS-B-SS) (Fig. 2B). Two other males sang both a northern theme song and a southern theme song.

At six locations we encountered small flocks of White-crowned Sparrows, some of whom sang quiet, quavering songs clearly identifying them as *Z. l. gambelii*, migrating through the area to breed in northern BC or Alaska. Their songs are not included in any analyses.

VARIATION IN TERMINAL TRILLS

Like Baptista (1977) and Heinemann (1981), we use the terminal trills of White-crowned Sparrow songs to distinguish among regional song dialects. Virtually all terminal trills can be categorized without ambiguity, and so we have used

the numbering scheme of Baptista (1977) and DeWolfe and Baptista (1995) to denote trill types, and hence dialects (Fig. 3). The distribution of these trill types is given in Table 1.

TABLE 1. Distribution of terminal trill types used in distinguishing among song dialects. Bilingual males with two different trill types appear twice. Locality numbers correspond to Figure 1 and to notations in text; localities listed from south to north. Trill type numbers correspond to Figure 3.

Locality*		No. of males singing trill type					
No.	Name	2	3	5	6	8	9
1	Tokeland	2		3			
2	Grayland		1				
3	Westport			4			
4	Ocean Shores			3			
5	Ocean City			7			
6	Kalaloch			1			
7	Forks				1		
8	Neah Bay			3			
9	Sekiu	1		2			
10	Pysht			2			
11	Hoodsport			3			
12	Tacoma			6			
13	Seattle			6			
14	Poulsbo			7			
15	Kingston			2			
16	Port Gamble			2			
17	Edmonds			1	2		
18	Freeland					7	
19	Camano I.			1		9	
20	Coupeville			5		4	7
21	Port Townsend					1	
22	Port Angeles		3		3		
23	Sequim				3		
24	Bellingham		1		10		
25	Burlington				4		
26	Anacortes				7		
27	San Juan I.		1		29		
28	Port Renfrew				3		
30	Victoria		1		5		
31	C. Saanich				6		
32	Maple Bay				5		
33	Ladysmith				4		
34	Nanaimo				11		
35	Parksville				8		
36	Port Alberni				1		
37	Comox				2		
38	Campbell R.				1		
39	White Rock				3		
40	Vancouver				9		
41	Gibsons				3		
42	Sechelt		1		5		
43	Madeira Park		1		3		
44	Egmont				1		
45	Saltery Bay				2		
46	Powell R.		1		4		
Total		4	4	63	139	21	7

* No terminal trills were recorded in locality 29, River Jordan.

As in other populations of White-crowned Sparrows (e.g.: *Z. l. oriantha*, Lein 1979; *Z. l. nuttalli*, Petrinovich 1988), not all males finish each song with a trill. Some well-studied males sing songs that consistently lack a terminal trill (Petrinovich 1988, Chilton et al. 1990). Therefore the number of trills indicated in Table 1 is smaller than the number of singers recorded in some localities.

In the earlier surveys of Baptista and Martin, dialects 5 and 6 had the largest ranges, essentially the Olympic Peninsula of WA (dialect 5), and Vancouver I. and mainland BC (dialect 6) (Fig. 1 in Baptista 1977). The transition from one dialect to the other was apparently abrupt. At that time, all males in Sequim (loc. 23) sang dialect 5, while all males in Port Townsend (loc. 21), 25 km away, sang dialect 6. Baptista (1977) did not record both dialect 5 and 6 in any locality.

We recorded dialect 6 in all localities where it had been recorded by Baptista (1977). We also recorded this dialect between Powell River (loc. 46) and Gibsons (loc. 41), and on the north shore of the Strait of Juan De Fuca; these localities were not visited by Baptista and Martin. Dialect 6 has spread beyond the range reported by Baptista (1977) and Baptista and Martin (unpubl. data) to include the communities of Edmonds (loc. 17), Sequim (loc. 23) and Port Angeles (loc. 22), previously occupied by dialect 5 singers. This represents a range expansion of dialect 6 of approximately 35 km to the south and 50 km to the west.

We recorded dialect 5 from males in seven localities north of the distribution reported by Baptista (1977), including Madeira Park (loc. 43), 200 km northwest of Sequim (loc. 23). However, in each of these localities, we recorded only one bird singing dialect 5 while all other males sang dialect 6. Excluding males singing these extralimital songs, the distribution of dialect 5 is approximately the same as found by Baptista (1977) and Baptista and Martin (unpubl. data), having retreated tens of kilometers with the advance of dialect 6.

Baptista (1977) recorded dialect 4 from 22 males in four localities near Grays Harbor, WA in 1970. We recorded 30 males in five localities in this region in 1994, but did not encounter any males singing dialect 4. With the exception of one male that sang dialect 3, one that sang dialect 2, and one bilingual male that sang both dialects 2 and 5, all males in this region sang dialect 5 (Table 1).

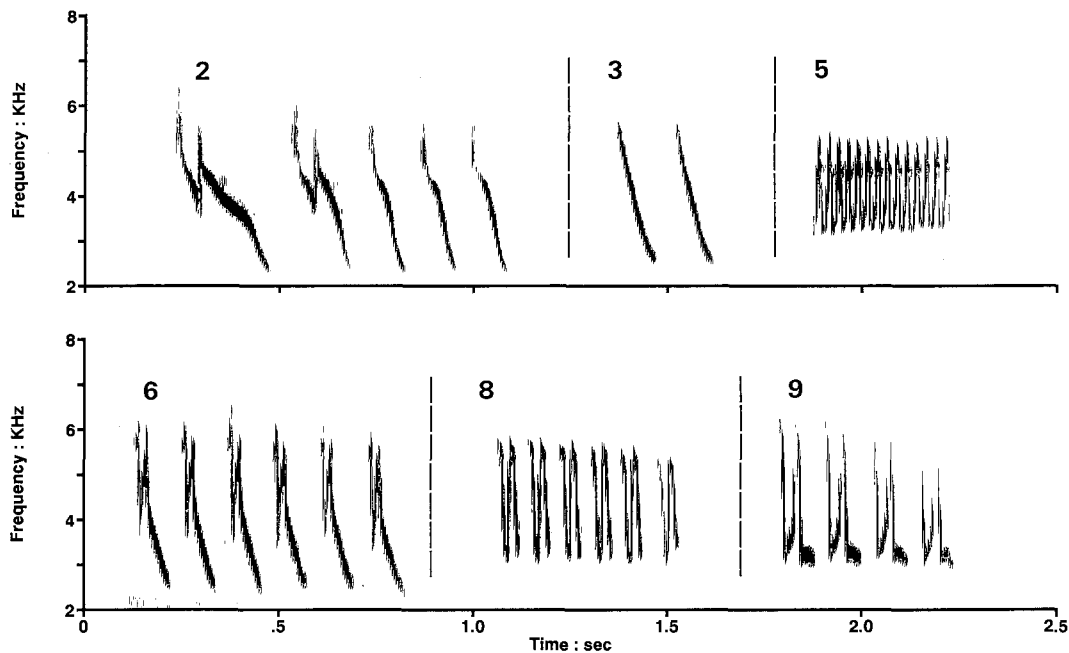


FIGURE 3. Lexicon of terminal trill types used in distinguishing among song dialects. Trill types 2, 3, 5, and 6 were also reported by Baptista (1977). Trill types 8 and 9 are new to this study.

We recorded dialect 3 from three males in Port Angeles (loc. 22), far north of its previously-reported range near the Washington/Oregon border. The closest community in which Baptista (1977) recorded dialect 3 was Long Beach, WA, 200 km south of Port Angeles.

Baptista (1977) recorded dialect 2 (southern theme) from males in 10 localities in northwest Oregon. We recorded this dialect from one male in Sequim (loc. 23), and from bilingual singers in Tokeland (loc. 1) and Powell River (loc. 46).

We recorded two distinctive trill types (Fig. 3) that were not reported by Baptista (1977). They are categorically different in structure from other trill types, and so we designate them as new dialects. Dialect 8 was recorded in Port Townsend (loc. 21), Coupeville (loc. 20), Freeland (loc. 18), and Camano I. (loc. 19). Dialect 9 was recorded only in Coupeville. Port Townsend was the only one of these communities visited by Baptista (1977) or Baptista and Martin (unpubl. data).

We also found subtle variation in the trills of songs of dialect 6 (Fig. 4). These terminal trill variants differ in their tempo, and the length and shape of the downward sweeping tail. Subdialect 6B appears to be intermediate in structure be-

tween 6A and 6C. Even though there is some overlap in the geographic distribution of the trill type 6 variants, we consider them to be "subdialects." The distribution of these subdialects of dialect 6 is given in Table 2. Only the best recordings permitted us to categorize trill type variants, and therefore the number of singers on Table 2 is smaller than the number of trill type 6 singers on Table 1 for some localities.

Even though small sample size limits our ability to describe the specific distribution of subdialects, some patterns are apparent (Fig. 5). Subdialect 6C was recorded most often on the east side of the Strait of Georgia, while 6A and 6B were recorded on the southwest and northwest sides, respectively. Subdialect 6D was most common at the northern limits of the subspecies, while 6E was recorded in four localities across the mouth of Puget Sound.

Baptista (1977, Fig. 3) also found variation in dialect 6 terminal trills, and denoted these variants as 6a through 6d. Our letter designations for variants of dialect 6 do not correspond to his. Baptista (1977) also found some evidence of regional distribution of these variants; his 6b was more common on south Vancouver I., while 6c and 6d were more common in the north.

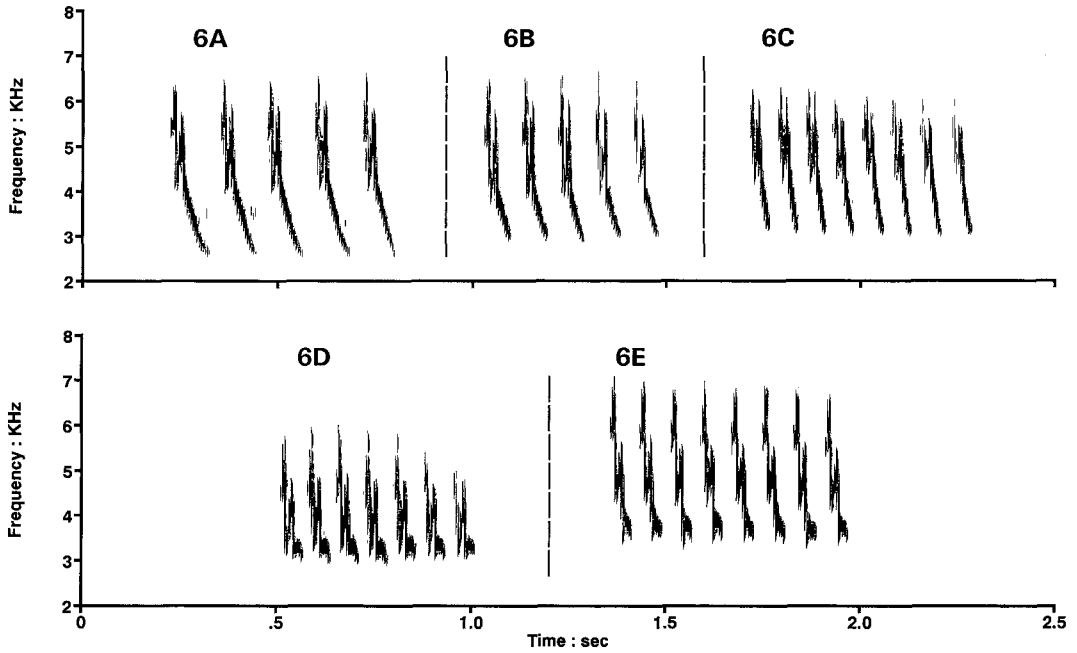


FIGURE 4. Lexicon of terminal trill type 6 variants used in distinguishing among subdialects.

TABLE 2. Distribution of variants of terminal trill type 6 used in distinguishing among subdialects. Locality numbers correspond to Figure 5. Variant letters correspond to Figure 4.

No.	Locality Name	No. of males singing trill variant				
		6A	6B	6C	6D	6E
17	Edmonds	1		1		
21	Port Townsend					4
22	Port Angeles	3				
23	Sequim					3
24	Bellingham			8	1	1
25	Burlington			1		
26	Anacortes			6		1
27	San Juan I.	3	19	3		
28	Port Renfrew				2	
30	Victoria	4	1			
31	C. Saanich	6				
32	Maple Bay	4	1			
33	Ladysmith		3			
34	Nanaimo		6	5		
35	Parksville		1	3		
37	Comox				2	
38	Campbell R.				1	
39	White Rock			3		
40	Vancouver			7		
41	Gibsons				2	
42	Sechelt			3		
43	Madeira Park			2		
44	Egmont					1
45	Saltery Bay					2
46	Powell River					2
Total		21	31	42	13	9

VARIATION IN OTHER SONG COMPONENTS

Virtually all males that sang northern theme songs included two complex syllables between the first and second buzzes. A few males consistently produced songs with either one or three complex syllables, and some produced successive songs with one and two, or two and three complex syllables. Baptista (1977) reported similar variation. Generally, the paired complex syllables in a song were identical, although some males consistently sang songs containing two different complex syllable types.

Not all complex syllables can be categorized without ambiguity because there is substantial gradation between some types. We have divided the complex syllables recorded in this study into eight types based on their structure (Fig. 6). The distribution of these types is given in Table 3. The numbers that we use to denote complex syllable types in this study do not correspond to the numbers used by Baptista (1977). Because some males sang more than one song type which differed in their complex syllables, and each syllable is tallied separately, the number of complex syllables reported in Table 3 exceeds the number of males recorded in some localities.

We recorded some complex syllable types over

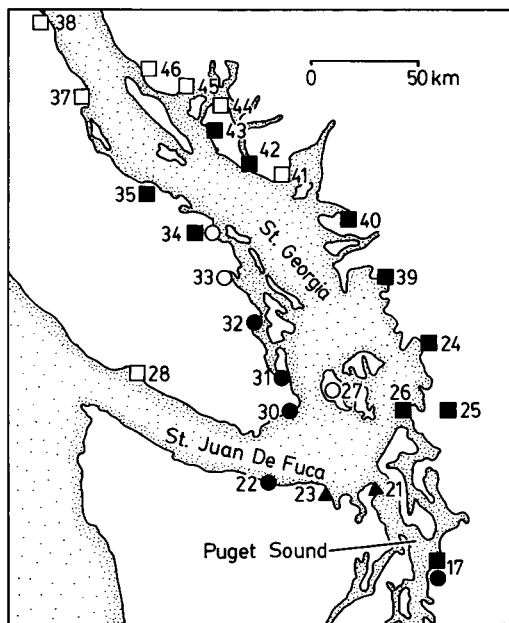


FIGURE 5. Distribution of subdialects within dialect 6. Locality numbers correspond to Table 2. Symbols represent the most common subdialect in each locality: closed circle = subdialect 6A; open circle = subdialect 6B; closed square = subdialect 6C; open square = subdialect 6D; closed triangle = subdialect 6E. Two subdialects were equally common in localities 17 and 34.

very large areas (e.g., type 3), while others were highly localized (e.g., type 6). Although some complex syllable types were more common in northern regions (e.g., types 1 and 2), and others were more common in south (e.g., type 5), we did not find discrete distributions of complex syllable types as we found with terminal trill types.

Baptista's (1977) complex syllable types 3, 6, and 8 are similar to our types 6, 1, and 8, respectively. We did not encounter Baptista's complex syllable type 1, which had an extensive distribution in 1970, nor did Baptista encounter our syllable type 5 which had an extensive distribution in 1993 and 1994. It appears that the majority of complex syllables recorded by Baptista (1977) had no counterpart in the current study, and the majority of complex syllable types which we recorded were not encountered by Baptista.

It seems as though some complex syllables, even common types with wide distribution, are not as persistent in the long term as are terminal trill types. However, we have an example of the persistence of one complex syllable type with

very limited distribution. Baptista's complex syllable type 3 was recorded in 1970 from 26 of 65 males on San Juan I. (loc. 27) and nowhere else. This syllable appears to correspond to our syllable type 6, which we recorded in 1994 from 23 of 33 males on San Juan I., and from one of eight males in Central Saanich (loc. 31), 20 km from San Juan I., in 1993.

Like Baptista (1977), we recorded a number of "exceptional songs," including those with two terminal trills rather than one, and the substitution of a whistle for the second buzz. These exceptions are within the variation expected in a large sample of White-crowned Sparrow songs, and do not appear to be local phenomena. In contrast, a group of individuals in one region used exceptional second buzzes. In the present study, both the first and second buzzes of the songs of virtually all males showed little variation in mean pitch (Fig. 7A-C). The exceptions are the downward-sloping second buzzes (Fig. 7D-F) given by most males in five localities in the region of Grays Harbor (Table 4). A few birds in this same region sang downward-sweeping buzzes in 1970 (Baptista pers. comm.).

DISCUSSION

CHANGES TO *PUGETENSIS* SONG TYPES AND DIALECT BOUNDARIES

The two song dialects (5 and 6) that Baptista (1977) and Baptista and Martin (unpubl. data) found to have the widest geographical distribution in 1970 and 1977 have survived many generations of cultural transmission to the present study without any apparent change in the structure of their terminal trills. While these workers reported a relatively abrupt boundary between these dialects, we recorded five birds singing dialect 5 in localities dominated by dialect 6, far north of the original boundary. If these extralimital songs are ignored, then the boundary between dialects 5 and 6 appears reasonably abrupt, as it did in the earlier surveys. However, dialect 6 is now heard in localities 35 km south and 50 km west of its apparent limits in earlier studies.

Dialect 4 was recorded in just four localities in the vicinity of Grays Harbor in 1970 (Baptista 1977). Virtually all males in this vicinity sang dialect 5 in 1994, and dialect 4 was not encountered. Grays Harbor is at the southern edge of our survey area, and dialect 4 may still be produced by birds in areas that we did not visit. Whatever population processes caused the range expansion of dialect 6 to encompass localities

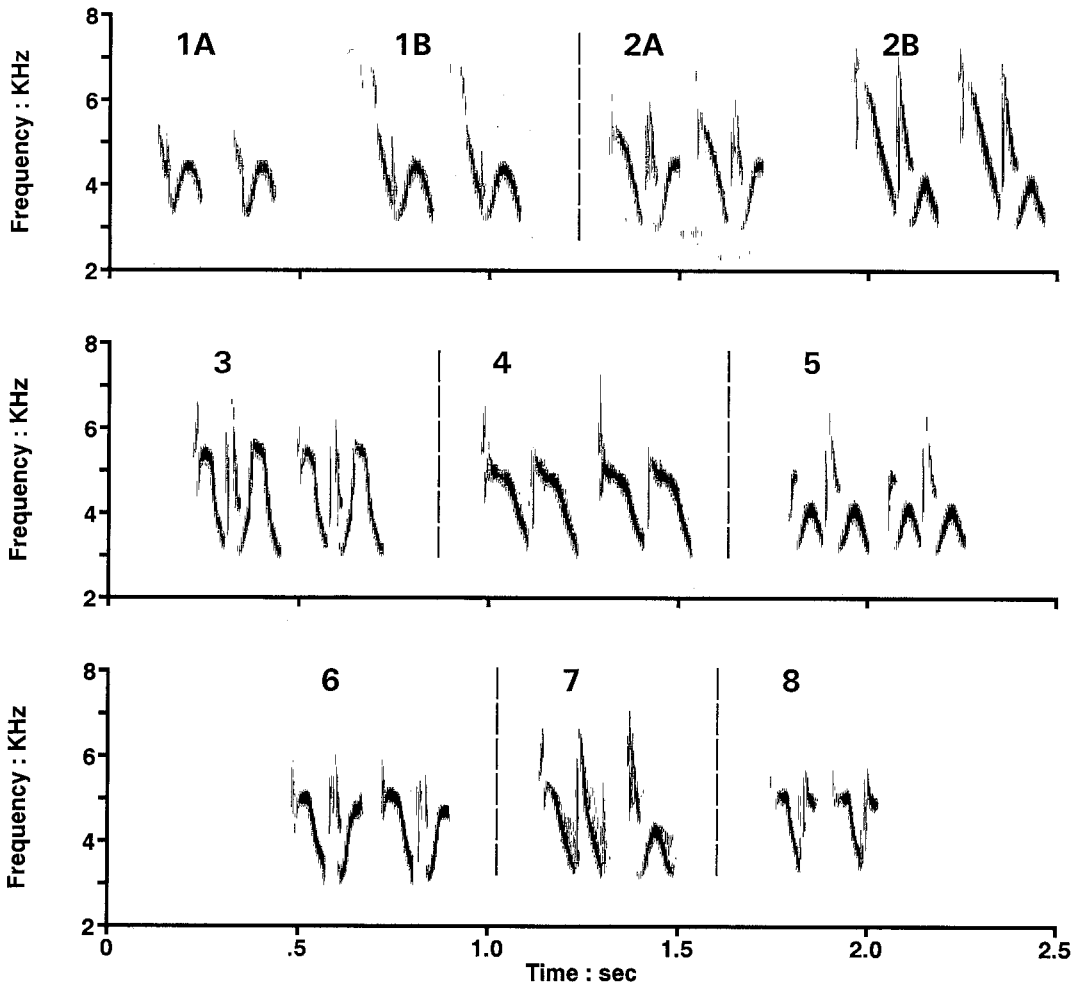


FIGURE 6. Lexicon of complex syllable types of northern theme songs.

previously occupied by males singing dialect 5, may have also caused dialect 5 to expand south to encompass localities previously occupied by males singing dialect 4.

Because song is a learned behavior, novel song components probably result from learning errors and innovation (Slater 1986, Catchpole and Slater 1995). The generation of a new component may result from a single, substantial change from the parental form, or from the accumulation of smaller changes. Jenkins (1978) referred to the origin of new song patterns that are transmitted accurately between generations as "cultural mutations." Heinemann (1981) was unable to find any substantial variation in the songs of *Z. l. pugetensis* not already reported by Baptista

(1977), and concluded that our knowledge of song variation in this subspecies was nearly complete. Here we report two previously-undescribed song dialects.

We recorded terminal trill type 8 in the neighboring localities of Freeland (loc. 18), Camano I. (loc. 19), Coupeville (loc. 20), and Port Townsend (loc. 21), and trill type 9 only in the vicinity of Coupeville. These trill types may represent "cultural mutations" that have arisen since the studies of Baptista and Martin, or they may have been brought, intact, by individuals dispersing from areas not yet surveyed. Baptista (pers. comm.) found birds singing terminal trills similar to our type 9 on San Juan I. (loc. 27) and in Vancouver (loc. 40) in 1970, but combined these

TABLE 3. Distribution of complex syllable types, excluding southern themes. Bilingual males with two different complex syllable types appear twice. Locality numbers correspond to Figure 1. Complex syllable type numbers correspond to Figure 6.

No.	Locality Name	No. of males singing complex syllable type							
		1	2	3	4	5	6	7	8
1	Tokeland			5					
2	Grayland				1				
3	Westport			9					
4	Ocean Shores			4					
5	Ocean City		2	7		1			
6	Kalaloch			1					
7	Forks	1		1					
8	Neah Bay			2		2			
9	Sekiu			2					
10	Pysht			3					
11	Hoodsport			4		1			
12	Tacoma			6		3			
13	Seattle			5	1	1			
14	Poulsbo			7					
15	Kingston			3					
16	Port Gamble			4		1			
17	Edmonds	2		2					
18	Freeland			4					
19	Camano I.			11		1			
20	Coupeville		3	9					
21	Port Townsend			4		3			
22	Port Angeles			7					
23	Sequim		1	2					
24	Bellingham	11		1					
25	Burlington	1		1	3				
26	Anacortes			6		1			
27	San Juan I.		1	9	1		24		1
28	Port Renfrew		3						
29	River Jordan			1					
30	Victoria	3	3	3					
31	C. Saanich	3		4			1		
32	Maple Bay	5	1						
33	Ladysmith	4							
34	Nanaimo	11	2						
35	Parksville	3	6		1				
36	Port Alberni		3	1					
37	Comox		3	1					
38	Campbell R.		1	1	1				
39	White Rock	5							
40	Vancouver	8	2			4			
41	Gibsons	1	3	1				1	
42	Sechelt	4	2	1					
43	Madeira Park		4	2					
44	Egmont		1						
45	Saltery Bay		2						
46	Powell River		7						
Total		62	50	134	8	18	25	1	1

songs with trill type 6. At present, we are unable to resolve the between-survey difference in distribution of trill type 9. A wintering male singing a terminal trill similar to our type 8 was recorded in San Francisco, CA (Fig. 1C in Baptista et al. 1993; reprinted as Fig. 5D in DeWolfe and Bap-

tista 1995), although this type has not been recorded previously from males in the breeding season.

Baker (1975) proposed a scenario for the origin of new song types in *Z. l. nuttalli* and *Z. l. oriantha* involving the colonization of unoccupied

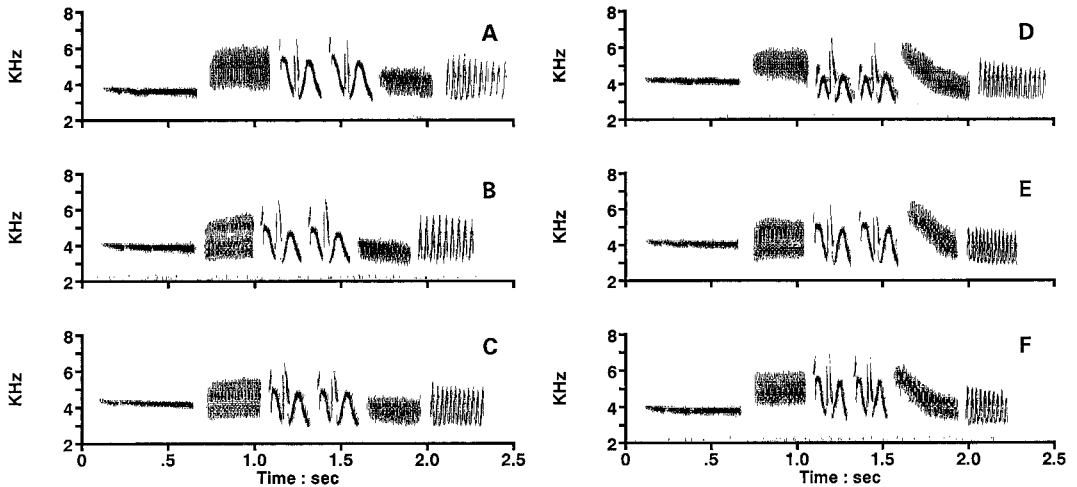


FIGURE 7. Variations in form of second buzzes used in northern theme songs. A-C. Typical northern theme songs, D-F. Songs in which the second buzz is downward-sloped.

habitat. In this scenario, a habitat change, such as a fire, causes a local population of birds to go extinct. With regeneration of the habitat, the region is recolonized. The first male colonists might invade before the termination of their song learning, and improvisation results in songs that are different from those of the parental stock. Philopatric offspring of those first colonists perpetuate the new song (Baker 1975), and juveniles dispersing to this area acquire the new song while interacting with established males (Baptista pers. comm.).

We cannot reconstruct the origins of trill types 8 and 9 with confidence, but Baker's scenario involving allopatric cultural evolution seems unlikely here. The localities that contained males singing those song types appeared to us to be

occupied by a greater density of White-crowned Sparrows than anywhere else on our survey. Most of the habitat between sampling localities has been modified by human activity, and appears to be suitable for occupation by White-crowned Sparrows. It is hard to imagine that *pugetensis* populations in this region are isolated in any meaningful way. We think it more likely that dialects 8 and 9 originated in sympatry with other trill types.

Trill types 8 and 9 were heard in localities near the point of contact between dialects 5 and 6. Trill type 8 has a tempo similar to that of type 5, and elements with the three-part construction typical of trill 6, and may represent a "hybrid" of the two. Trill type 9 is similar to trill type 6D, and may be a variation on it. Because we found no gradation of one trill type into another, we feel justified in describing them as distinct dialects.

Whatever the origin of new song types, their survival is likely enhanced by isolation. Individuals of *Z. l. nuttalli* are non-migratory, and maintain territories year-round. For members of this subspecies, channels of water as narrow as 0.5 km may serve as barriers to dispersal, and help to explain the existence of unique song dialects on islands in San Francisco Bay (Baptista 1975). In contrast, Baptista (1977) found that *pugetensis* on Vancouver I. and San Juan I. sang the same song dialect as did males recorded on the main-

TABLE 4. Distribution of northern theme songs with downward-sloping second buzzes. All localities are near Grays Harbor, WA. Locality numbers correspond to Figure 1.

No.	Locality Name	No. of males with second buzz types	
		downward-sloping	constant-pitch
1	Tokeland	1	4
2	Grayland	1	0
3	Westport	8	1
4	Ocean Shores	4	0
5	Ocean City	9	0

land, and concluded that there must be some dispersal of individuals between mainland and island populations in this migratory subspecies.

Even so, the pattern of distribution of subdialects of dialect 6 reported in the present study suggests that the Strait of Georgia may provide considerable geographical isolation with concomitant cultural isolation. Subdialects 6A and 6B were recorded most commonly on the west side of the Strait, while 6C and 6D were most common on the east side (Fig. 5). Dispersal across the Strait is probably sufficiently rare to allow the formation of subdialects. On the west side of the Strait of Georgia, subdialect 6A intergrades with 6B in Victoria (loc. 30) and Maple Bay (loc. 32), and 6B intergrades with 6C in Nanaimo (loc. 34) and Parksville (loc. 35) (Fig. 5). If we consider subdialect 6B as an intermediate between 6A and 6C, then distance may also provide sufficient isolation to allow divergence of song.

We recorded a few males singing specific dialects in localities far from the 1970/1977 distribution of those dialects. These include the five males singing dialect 5, as described above, three males in Port Townsend (loc. 21) singing dialect 3, and three males singing dialect 2 in widely-scattered localities. Baptista (1977) reported no such extralimital singers in his 1970 survey, but recorded a number of males singing "hybrid" songs with components from both northern and southern themes. These hybrid songs were recorded in populations at some distance from zones of contact between themes (Baptista 1977). We did not record any singers of hybrid songs.

There are several possible explanations for the males we observed singing extralimital songs. First, dialect boundaries may not be as sharp as we believe, but sampling (as opposed to censusing) means that some rare song types are overlooked. However, failure of the earlier surveys to find *any* males singing song dialects far outside the normal limits of those dialects suggests to us that our study differs in some way from those of Baptista and Martin.

Second, our surveys were conducted earlier in the year (April and May) than those of Baptista (1977) (June and July). We cannot exclude completely the possibility that some of the birds we recorded were migrating, and had not yet established breeding territories. However, we find this explanation for extralimital singers improbable. Unlike the quiet, quavery songs of *Z. l. gambelii*

migrants we encountered, all *Z. l. pugetensis* males sang complete, loud songs, and responded strongly to song playback. Frequently, we observed a second, non-singing bird in the vicinity of the singer. This second bird was presumably the mated female, suggesting that breeding territories had been established. Blanchard (1941) described the period from 10 to 14 April as the peak arrival time of male and female White-crowned Sparrows to breeding territories on San Juan I. (loc. 27), near the midpoint of our study range. This is 10 days before our earliest recording. Further, all of our extralimital singers were found *north* of the normal limits of dialects they sang, suggesting that they were not northward-bound migrants.

A third possible explanation for males singing extralimital songs involves our early recording dates. Many male White-crowned Sparrows in their hatching-year hear the songs of older males from a number of different dialect populations on the wintering ground. Some of these young males use more than one song type while establishing their first breeding territory, but subsequently delete all but one type after interacting with males on adjacent territories (Baptista and Morton 1988, DeWolfe et al. 1989). At least two of our extralimital singers were bilingual, singing the local song type and a song type typical of males in distant populations. Others were not heard to sing the local song type (Chilton and Lein 1996). If we had conducted our surveys later in the season, after considerable countersinging between adjacent territory holders, it is possible that some of these males would have ceased to sing that alien song type, using only the local song type.

A final explanation for birds singing song types far beyond the normal distribution of these types involves habitat changes resulting from the increasing human population of this region. Like *Z. l. nuttalli*, *Z. l. pugetensis* is most often found near human habitation (Baptista 1977, this study). In this study, White-crowned Sparrows were heard most commonly near marinas and ferry terminals, shopping mall parking lots, small farms, and city parks. A few males were recorded in clear-cut forest lots, and suburban neighborhoods. The human population of Puget Sound and southwestern BC has expanded greatly since Baptista and Martin's surveys. Perhaps this has created new White-crowned Sparrow breeding

habitat at a very rapid rate. Vacancies may have been occupied by birds dispersing far from their natal population who found few neighbors, and therefore were under little pressure to match their song to the local dialect (Baptista and Morton 1988, Lein, Chilton and Walker unpubl. data).

OTHER STUDIES OF CHANGES TO SONG TYPES AND DIALECT BOUNDARIES

Most studies that have compared the songs of a species over a period of several years have emphasized changes to songs, rather than the persistence of song types. Thompson (1970) recorded the songs of 82 male Indigo Buntings (*Passerina cyanea*) in Michigan in 1965 and 1967. Even though young copied the songs of neighbors when attempting to establish territories, there was considerable change in song. Of 98 figure types recorded in the study, 20 were recorded in 1965 only, while 22 were recorded in 1967 only.

Most dialect populations of Indigo Buntings consist of two to five (as many as 12) males (Payne et al. 1981). Over a 15-year study, a few song types persisted, but most did not survive in a recognizable form. However, the half-life of songs was roughly three times longer than the half-life of individuals. Song types were perpetuated when males copied songs of territorial neighbors, shortly after their arrival in spring.

Male Village Indigobirds (*Vidua chalybeata*), have repertoires of more than 20 song types (Payne 1985). Each song type changed from year to year as males modified their songs to match others, and the accumulation of changes rendered types unrecognizable in five years. Payne (1985) observed both the expansion of song populations, and the extinction of song types.

Male Great Tits (*Parus major*), sing repertoires of one to eight songs (McGregor and Krebs 1982). In a six-year study, both increases and decreases in the number of males singing particular song types were documented. Some songs were common one year, but absent in both the preceding and following years.

Examples of the long-term persistence of song types are less common. Trainer (1983) found that the basic structure of two dialects of White-crowned Sparrows (*Z. l. nuttalli*) in Berkeley Hills, CA did not change in 18 years. Baker et al. (1984a) compared their recordings of *Z. l. nuttalli* near Point Reyes, CA, to those of Marler and Tamura

(1964), and found no change over 25 years. Baptista (pers. comm.) documented both long-term persistence and elimination of song types among *Z. l. nuttalli* in Richmond, Brooks Island, Lake Merced, and Golden Gate Park, CA. "Hybrid" songs, incorporating syllables from two distinctive song types, sometimes arise at a point of contact between White-crowned Sparrow dialects (Lein and Corbin 1990, Baptista and Gaunt 1994). Specific song dialects of the Rufous-collared Sparrow in Argentina have persisted for 20 years, and perhaps much longer (Handford 1981, 1988).

McGregor (1980) found that the boundaries between three song dialects of Corn Bunting (*Emberiza calandra*) remained stationary for three years, but attributed this stability to the high rate of survival of individual territorial males.

Handford (1981, 1988) showed that the sharp boundaries between Rufous-collared Sparrow song dialects, which appear to coincide with changes in habitat type, remained stable for at least 20 years. The location of a cline between trill dialects of the Rufous-collared Sparrow in eastern Argentina remained stable over at least six years; loss of the "talar" dialect was attributed to habitat alteration (Tubaro et al. 1993).

Trainer (1983) documented the movement of a boundary between two dialects of a non-migratory subspecies of White-crowned Sparrow. The dialects of *Z. l. nuttalli* are very localized, and the boundary movement was on the order of hundreds of meters in ten years. Long-term changes in dialect distribution were linked to specific changes in habitat. The dialects came into contact with the creation of a golf course, and one dialect may have displaced the other as a result of chance events during a population bottleneck resulting from a drought (Trainer 1983).

In the intergrade zone between *Z. l. pugetensis* and *Z. l. nuttalli*, the boundary between song types may have remained stationary since secondary contact after the Pleistocene, while morphological, physiological, and electrophoretic traits have moved south (Baker et al. 1984b, Baker 1987). To date, most studies have demonstrated the permanence of boundaries between song dialects. The present study shows that the boundaries between dialects of *Z. l. pugetensis* can move at a rate of kilometers, or tens of kilometers, per decade.

PROCESSES RESPONSIBLE FOR
CHANGE IN LOCAL SONG
TRADITIONS

Cultural evolution, like genetic evolution, is driven by mutation, migration, drift, and selection (Lynch et al. 1989). With regard to song, migration refers to immigrants that bring new song traditions with them (Payne et al. 1981). Mutation of song components includes learning errors, innovation, and the recombination of song elements (Baptista and Morton 1988, DeWolfe and Baptista 1995).

Lynch et al. (1989) considered song units of Chaffinches to be "neutral," likening them to the "neutral alleles" of a gene. Forms of a syllable, for instance, are believed to be functionally equivalent, and not subject to selection for one over another. Changes would result from the cultural equivalent of genetic drift.

In a number of species, including the White-crowned Sparrow, males establishing their first breeding territory may alter their songs to match the songs of neighboring males (Baptista and Morton 1988). There may be some social advantage to singing the local song type rather than a type characteristic of a more distant population (Baker and Cunningham 1985). There is no reason to suppose that birds in a population share a song type *because* that particular song type provides a selective advantage over any other song type.

Song variants are not necessarily selectively neutral in all species. Gibbs (1990) found changes in the incidence of four song types of male medium ground finches (*Geospiza fortis*) over a six-year period, and related these to selective pressures, both direct and indirect, on singers of those song types. Sons inherited their fathers' song type, and singers of less-common songs lived longer and produced more offspring. Grant and Grant (1995) related changes in song type frequency in large ground finches (*G. magnirostris*) to chance differences in recruitment success among males in a small population, as a cultural equivalent of genetic drift.

Z. l. pugetensis dialects are probably selectively-neutral versions of the species-specific song. Each *pugetensis* dialect is heard in a variety of habitat types, from trees lining busy city streets, to clear-cut forest lots. Like Baptista (1977), we found no evidence that the boundary between song dialects corresponded to a change from one

habitat type to another. The long-term changes we observed in song type distribution are not likely to have resulted from selection for individuals singing one song type over those singing another type. Rather, changes are probably the result of population changes that are not linked directly to variation in song.

ACKNOWLEDGMENTS

We are grateful to Luis Baptista for sharing his thoughts and unpublished observations, and to Paul Handford and an anonymous reviewer for their comments on an earlier version of this manuscript. This research was supported by a Natural Sciences and Engineering Research Council of Canada operating grant to MRL.

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