

Does learning produce song conformity or novelty in white-crowned sparrows, *Zonotrichia leucophrys*?

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Song learning in birds makes it possible for males to faithfully imitate tutors and also to generate novel improvisations. Within local dialects of the Puget Sound white-crowned sparrow, most males share the terminal trill phrase in their songs. In contrast, the introductory note complex is more variable within local populations and appears to encode individual identity. We studied the song-learning process during initial territory establishment in a wild population of white-crowned sparrows. Although most adult males sing a single song type, many yearling males overproduce song types early in their first singing season before deleting all but one song type from their repertoire. We asked whether this attrition process favours retention of a song with a note complex that resembles that of a male's neighbour, as would be predicted by various hypotheses assuming a benefit to song sharing, or whether it favours retention of a distinctive note complex, which would produce individuality in song. We found that males that initially overproduced song types retained shared note complexes, and that these males were more likely to share their adult note complex with neighbours than were young males that did not overproduce. Only 51% of recruits overproduced, however, and we close by speculating that overproduction and close song sharing may be correlates of male quality and learning ability.

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Song learning in birds, a familiar example of a socially learned behaviour, can produce either conformity with a stimulus, as when a young pupil models its song(s) on those of one or more tutors, or novelty, if the young bird improvises or invents his song (Marler & Peters 1982c; Slater & Lachlan 2003). Song conformity resulting from imitative learning has been emphasized in previous research because it is the process leading to the formation of local song dialects or neighbourhoods, which may persist for many years (Podos & Warren 2007). The question of how individual males might benefit from sharing song(s) with their neighbours has attracted much research interest. Among the hypotheses often considered are that shared songs may be preferred by females, may address threat to specific receivers, may be deceptively mimetic, and serve as a badge of familiarity (Beecher et al. 1997). In contrast, song novelty may be favoured for different reasons, the most obvious being the advantage(s) to being individually recognizable (Tibbetts & Dale 2007). Individual recognition by song is universal, or nearly so, in songbirds (Lambrechts & Dhondt 1995; Stoddard

1996) and should be facilitated by unique acoustic 'signatures'. Individually distinctive song(s) may be advantageous in establishing and maintaining territories and/or could be favoured by a female mating preference for novelty. The goals of this paper are not to identify the function(s) of conformity or novelty in song, but rather to study the developmental mechanism(s) that produce conformity or novelty, and to describe the local geographical pattern in song structure that results from the learning process. Local clustering of songs has been shown in some populations of white-crowned sparrow (Cunningham et al. 1987; Bell et al. 1998; Nelson et al. 2001), but not in others (Trainer 1983; Nelson et al. 2001). However, none of these studies identified the particular song phrase(s) that varied on a local scale.

The white-crowned sparrow is well known for accurate imitation of song, which results in 'song dialects' (Marler & Tamura 1962; Kroodsma et al. 1984). One subspecies, the Puget Sound white-crowned sparrow, *Z. l. pugetensis*, forms a linear series of about 12 song dialects along the Pacific northwest coast of North America (Baptista 1977; Nelson et al. 2004). Most adult males sing a single song type typical of the local dialect, although as described below, 'overproduction' of two or more song types is common early in the breeding season (Nelson 2000). Two parts of the song, the note complex and the trill (Fig. 1), display different patterns of geographical variation. The terminal trill of the song varies little

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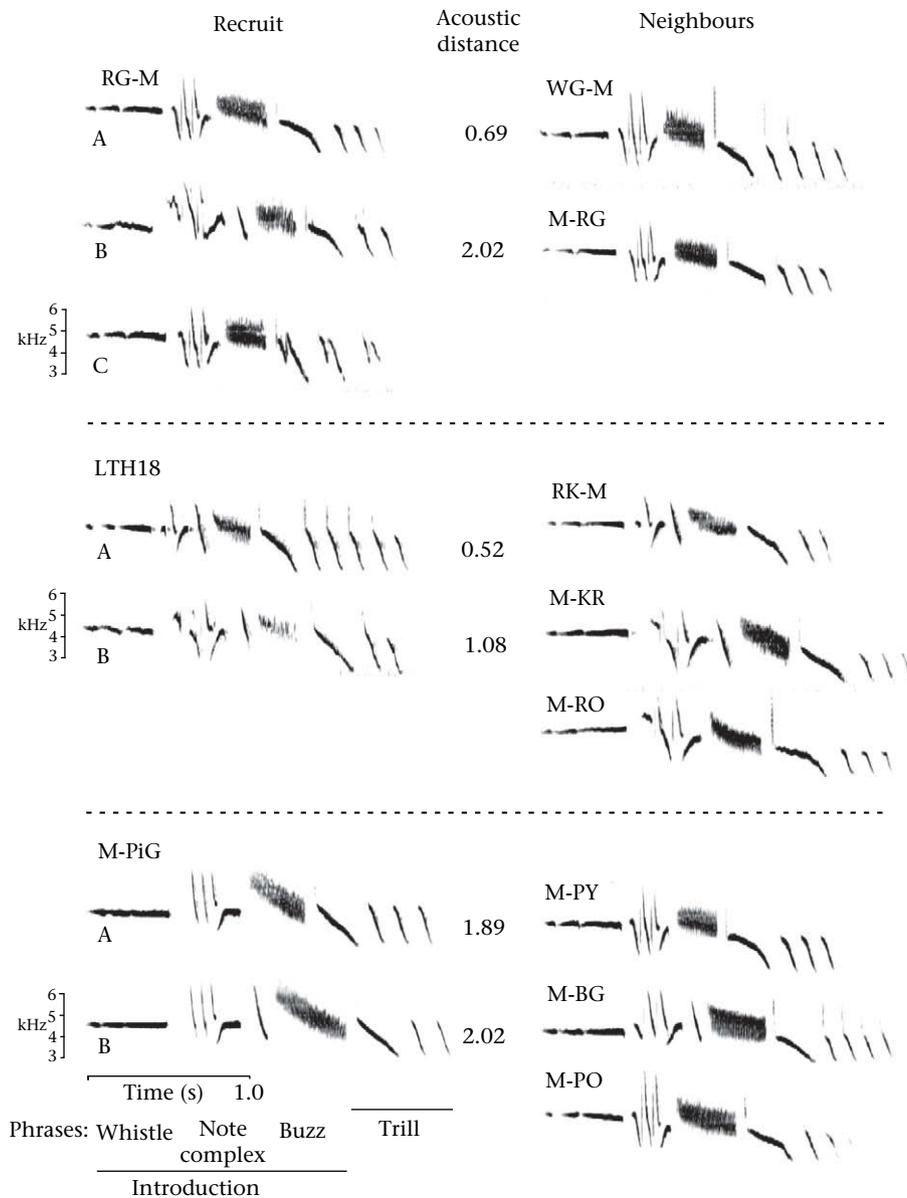


Figure 1. Examples of overproduced white-crowned sparrow song repertoires in three recruits (left column) and songs of their neighbours (right column). Song phrases are identified at lower left. Each recruit retained his song type A as his adult song type, which closely resembled at least one of his neighbours, and deleted the other type(s). Acoustic distances between the recruits' note complexes and the most similar neighbour's note complex are shown between the spectrograms. In most repertoires, the song types within a repertoire differed only in the note complex (RG-M's types A and B), but RG-M's types A and C were identical except for the trill, which is dialect 1 in type A and dialect 7 in type C. Recruit Lth18's two song types differed in all phrases, and we assume each was learned in its entirety from a different source. Recruit M-PIG's two note complexes were very similar, and differed only in the last frequency-downswept note. Both of these note complex types were sung by other males in the local population.

among most males at a given sampling location, and because of this, researchers use the trill to define the dialects. In a series of song playback experiments, male *Z. l. pugetensis* gave weaker responses to experimentally created songs containing foreign trills and local introductions than they did to control local songs or to songs with foreign introductions and local trills (Nelson & Soha 2004a, b). In contrast, the note complexes in the song's introduction are usually more diverse than trills within local populations (Nelson et al. 2004). Across the subspecies' range, 27 note complex 'types' have been described, and 10 of these are common (sung by > 5% of males) in our intensively studied population. Another experiment, using a neighbour-stranger discrimination paradigm, showed that males rely on the note complex in the song's introduction to recognize individuals (Nelson & Poesel 2007). Together

these observations and experiments suggest that the variable note complex in the introduction identifies individuals while the trill encodes information about the geographical source of a song, or its dialect.

Song learning in some sparrows consists of a two-stage process: young males first imitate, invent or improvise a number of song types and practise singing them. During the practise song stage, or plastic song, males then selectively retain one or more songs for their final adult repertoire, and discard the remainder (Marler & Peters 1981; Nelson & Marler 1994). As Beecher et al. (1997) have emphasized, the learning process is a selective one: males first choose one or more tutors to imitate for the initial overproduced repertoire, and then select a subset of those songs for the final repertoire.

In this paper we focus on the second, selective attrition phase. As studied so far in four species, the field sparrow, *Spizella pusilla*, chipping sparrow, *S. passerina*, white-crowned sparrow, *Zonotrichia leucophrys*, and song sparrow, *Melospiza melodia*, the selective attrition process results in song conformity: young males selectively retain song(s) that match those that their neighbours sing (Nelson 1992, 2000; Nordby et al. 2007; Liu & Nottebohm 2007). However, it is also possible that males could use the selective attrition process to choose songs that are dissimilar from those of their social partners (Marler & Peters 1982a). This outcome might be expected if the benefits of individuality outweigh those of song conformity. In particular, we focus on whether the selective attrition process results in the retention of a note complex that is individually distinctive in a local group of territory neighbours, or whether it results in note complex conformity. An earlier study on this species focused on selective sharing of the local dialect, and did not examine note complex sharing (Nelson 2000). Because the selective attrition process takes place when the young male establishes his first territory, deferring the final choice of song(s) until that point in time allows the male the flexibility to choose based on social conditions that may have changed from the time when he acquired his initial repertoire.

METHODS

Field Methods

We recorded male white-crowned sparrows at Bullard's Beach State Park, Oregon, U.S.A. The study site is a sand spit at the mouth of the Coquille River, approximately 3500 m long and 500 m wide. The study site is bounded on the west by the Pacific Ocean, to the south and east by the Coquille River and a marsh unsuitable for white-crowned sparrows, and to the north by woodland and low coastal dunes. The dunes to the north of our study site contained a relatively low density of breeding white-crowned sparrows. The birds breed in coastal dune habitat with European beach grass (*Ammophila arenaria*) as the dominant ground cover and nesting site and shore pine (*Pinus contorta*) as favoured song perches (Baptista 1977), and in a picnic area with a maintained lawn. Males arrive from their winter quarters in California beginning in late March. During each year of study, between 10 and 24% of the males had already arrived when we started field work on around 25 March. Females and yearling males arrive on average about 2 weeks after adult males (Nelson 2000).

The results in this report focus on four field seasons of intensive study between late March and June from 2005 to 2008. In addition, we recorded and banded males during visits in April of 2003 and 2004. We drove or walked through the study site every day, weather permitting, and recorded newly arrived males. We recorded 85 territorial males between March and June 2005, 76 males in 2006, 74 males in 2007 and 81 males in 2008. All were included in analyses of geographical variation within the study site, but since we lacked detailed data on initial repertoire size for some of these males, sample sizes are reduced for some analyses. Also, each year a few males that were present for less than 1 week were excluded from this analysis. Many of these, as judged by their dialects and behaviour, were migrants destined for more northerly breeding locations. We banded most males each year from 2005 to 2007 soon after their arrival with a unique combination of two colour rings and a numbered U.S. Fish and Wildlife band. Male sex was established by production of loud song, and later in the season, by the presence of a cloacal protuberance when a bird was captured. Yearling males can often be identified by plumage: those captured before 15 April were often still in head moult and retained brown feathers from their first basic plumage. These definite yearlings,

along with adult-plumaged males that occupied territories left vacant by banded males from the previous year are termed 'recruits'. In the mountain white-crowned sparrow, wing length increases significantly between the first and second breeding seasons (Morton 2002). As an additional indicator of age, we measured wing lengths of all captured recruits and compared them to 13 recaptured adult males that were present also in the previous year, termed here 'returns'. We also compared the arrival dates of males in different age classes to their breeding territories. To control for annual differences in arrival date, we subtracted the mean arrival date of all males in a given year from each male's arrival date.

From 2005 to 2007 we conducted 20 min focal watches on all males at least once per week from the date they arrived until they were paired (males stop spontaneous singing once paired). In 2008 we recorded males for 5–20 min on each visit. Males that overproduce typically repeat a song type four to five times before switching to a different type, so we are confident that the ad libitum sampling in 2008 detected most song types, typically two types, in each bird's repertoire. During each focal watch, we recorded all songs and dictated notes on the subject's behaviour. The focal watch recordings were then screened using the real-time spectrogram option in SIGNAL (Engineering Design, Berkeley, CA, U.S.A.) or Avisoft (Avisoft Bioacoustics, Berlin, Germany). Examples of distinct song types produced within a focal watch were saved as separate files for later analysis. We define a song type as an acoustically distinct song pattern that was sung repeatedly by a given male. Unique variants that were sung only once by a few birds were not counted as song types.

We recorded songs using a Sony TCD-D10 Pro II digital tape recorder (Sony Corporation, Tokyo, Japan) or a Marantz PMD670 solid-state recorder (Marantz Professional, Kanagawa, Japan) sampling at 48 kHz, 16-bit amplitude resolution, and Sennheiser MKH70 or ME67 'shotgun' microphones (Sennheiser, Wedemark, Germany) and Rycote windscreens (Rycote Ltd., Stroud, U.K.). Songs were digitized at or resampled to 25 kHz with 16-bit amplitude resolution using SIGNAL.

For each male, we selected the best quality recording of each song type in his repertoire for the analysis of geographical variation and selective attrition. Most overproducing males sang their song types loudly and with little acoustic variation within a type (i.e. the songs were crystallized). A few resident overproducing males were still in late plastic song in March, typified by relatively low song amplitude and a 'quavery' quality to note structure (e.g. song type B of male RG-M in Fig. 1). For each song, we digitally copied one note complex and the trill into separate computer files for analysis (see below).

Acoustic Variables

To describe acoustic variation within the local population, we used a set of variables that could be measured on both note complexes and trills, as described elsewhere (Nelson & Poesel 2007). In this population, most males sing a single, unrepeated series of notes grouped together in a note complex within the introduction, and end the song with a trill of repeated notes (Fig. 1). Our basic unit of analysis was the note, defined as a continuous tracing on an audiospectrogram longer than 5 ms and separated from other tracings by at least 3 ms. We chose variables such that we could draw a spectrogram of the sound from the measurements (the 'reconstruction criterion': Beecher 1989). We measured 17 variables on the first four notes in note complexes, and 12 variables on the first three notes in trills. We measured fewer variables on trills because the average trill contains three notes and trill duration varies greatly, from song to song and over the course of the

season (A. Poesel & D. A. Nelson, unpublished data). The number of variables chosen represented a compromise between the desire to describe the sound as completely as possible and the need to minimize the number of cases with missing data for phrases with fewer than four or three notes. Missing values were replaced with the population means for the given variable. We accepted Baptista's (1977) definition of the trill as all notes after the last buzz in the song, even though in the songs at Bullard's Beach, the first note after the buzz is distinct, and is not repeated to form a trill.

For each of the first four notes in the note complex and the first three notes in the trill, we measured: frequency at note onset, frequency at note ending, and note duration; and the quiet interval to the next note (the latter measure for all but the last note). In addition, we measured the total phrase duration, and calculated the mean note period (total phrase duration/number of notes). Because trill duration varies so much within males, we did not include number of notes and phrase duration in the analysis of trills. Measurements were made using a screen cursor and a program run in SIGNAL 4.04 on spectrograms (FFT length: 256 points; time resolution: 10 ms; frequency resolution: 98 Hz). Note onset and offset were measured at the point where amplitude was -21 dB relative to peak amplitude in the phrase.

Our analyses of song attrition and song sharing both required a measure of pairwise song dissimilarity or distance. We first used a principal components (PC) analysis to reduce the original set of measurements to a smaller set of uncorrelated PCs. Five PCs were sufficient to retain about 77% of the total variation present in the original set of variables measured on either note complexes or the trill. We then calculated acoustic distances as the Euclidean distance between pairs of songs in PC space (Nelson 1992).

Song Attrition Analyses

For the analysis of selective song attrition, for each song in a male's repertoire we calculated the minimum and mean acoustic distances to the songs of his immediate territory neighbours (birds that shared a boundary with the focal bird). We calculated acoustic distances separately in the PC space derived from the 17 measurements made on note complexes and in the PC space derived from 12 trill measurements. We compared the minimum acoustic distance between the retained song type and a neighbour's song to the minimum distance between the deleted song type and a neighbour's song using paired *t* tests (Nelson 1992). We also calculated the mean minimum acoustic distance to each of his neighbours' songs and the acoustic distance between the retained song type and a song chosen at random. For each male, we chose one non-neighbouring male in the population that sang the local dialect using the uniform random function (rounded to the nearest integer value) in SPSS 16. We calculated the acoustic distance between the phrase of interest in the retained song and the random song for each male and compared this distance to the distance between the retained and deleted phrases in a male's repertoire. For males that either retained or deleted two or more songs from their repertoires, we calculated the mean acoustic distance for all retained or deleted song types per male. All sample sizes are the number of males. Males that bred in several years were only included once in each analysis. We used nonparametric tests for comparisons where the data did not meet the assumptions of a *t* test. For parametric data, we report standardized effect sizes and 95% confidence intervals (Nakagawa & Cuthill 2007). We controlled the false discovery rate at 0.05 within a family of statistical tests using the Benjamini–Hochberg procedure (Benjamini 1995). This procedure maintains more statistical power in multiple comparisons than does the sequential Bonferroni procedure. Statistical computations were performed in SPSS 16.

Neighbour–Neighbour Sharing of Song Phrases

We used Mantel tests (Mantel 1967) to test whether acoustic variation was correlated with the spatial arrangement of singers in each population. The Mantel procedure correlates two matrices, with each matrix representing variation in a different dimension. The cells in one matrix contained acoustic distances between pairs of songs. For those males that sang two or more song types upon arrival before dropping all but one from their repertoire, we selected the song type that was retained throughout the breeding season for entry in the acoustic dissimilarity matrix. For males that sang two or more song types throughout the year, we used one example of each type. This acoustic dissimilarity matrix was correlated with a territory neighbour matrix. The cells in the territory neighbour matrix contained a '1' if the two males shared a territory boundary, and a '0' if they did not.

We used NTSYSpC (Rohlf 2000) to calculate Mantel correlations between acoustic distance and neighbour proximity for note complexes and trills in each of the 4 years. We used 10 000 permutations to calculate exact two-tailed probabilities. Because we performed eight tests (two phrases in each of 4 years), we used the Benjamini–Hochberg procedure to control the false discovery error rate at 0.05.

RESULTS

During 2005–2008, between 23 and 36 males bred each year for the first time in the study site and were classified as recruits. Each year between 36% and 57% of these recruits sang two or more songs types, or overproduced song, upon arrival in March and April (Table 1). In contrast, only 3–12% of returning males each year overproduced song, and several of these males defended territories throughout the entire study period. It is possible that we missed some song overproduction in 2005, when eight recruits were found within the first 3 days of field work; however in each of the 3 subsequent years, no more than two recruits arrived at the study site before we did. Of the 84 recruits captured or observed closely, 37 (44%) retained brown feathers in their crowns and were definite yearlings. There were 6–10 brown-crowned recruits each year. The black-crowned recruits may have been yearlings that completed moult earlier, or they may have been floaters or immigrant adults. We compared wing lengths and relative arrival dates of brown- and black-crowned recruits to known adults, which should have longer wings and earlier arrival dates than young birds. The wing lengths of returning adults were significantly longer than either brown- or black-crowned recruits (*t* test: $t_{40} = -4.48$, $P < 0.001$, 95% CI of effect size = 0.79, 2.19; $t_{55} = -2.59$, $P = 0.012$, CI = 0.27, 1.37, respectively; $P_{\text{critical}} = 0.036$ for the seven tests in this section; Table 2). Brown-crowned recruits had the shortest wing lengths, which did not differ significantly from black-crowned recruits ($t_{71} = -1.89$, $P = 0.06$, 95% CI = -0.02 , 0.93). Returning adults arrived about 9 days

Table 1

Total numbers of new recruits and returning male white-crowned sparrows each year (subtotals that overproduced are given in parentheses)

Year	Recruits	Returns	Incomplete data*	Total
2005	30 (17)	33 (1)	22	85
2006	24 (9)	46 (4)	6	76
2007	23 (10)	46 (5)	5	74
2008	36 (13)	44 (3)	6	81

* Birds on the margin of the study area for which we lacked accurate data on initial repertoire size or their experience. Their final song type(s) are included in the analysis of geographical variation.

Table 2

Wing length (mean and standard error) and arrival date of male white-crowned sparrows relative to the annual mean arrival date (medians with 25% and 75% quartiles) for two classes of new territory holders (recruits) compared to adults with prior breeding experience in the study site (returns)

	<i>N</i>	Wing (mm)	<i>N</i>	Relative arrival date (days)
Brown-crown recruits	29	69.7±0.29	33	2.0 (−6.2, 5.9)
Black-crown recruits	44	70.5±0.28	39	2.9 (−2.3, 15.0)
Returns	13	71.9±0.38	72*	−6.2 (−8.0, −2.7)

* For those returning males present in 2 or more years, we randomly selected the return date for 1 year.

earlier than either class of recruits (brown-crown recruits versus returns: Mann–Whitney *U* test: $U = 544$, $N_1 = 33$, $N_2 = 72$, $P < 0.001$; black-crown recruits versus returns: $U = 499$, $N_1 = 39$, $N_2 = 72$, $P < 0.001$). These are underestimates because 15–25 adults, but only 0–8 recruits, were already present each year when field work began. There was no difference in arrival date between the two groups of recruits ($U = 535$, $N_1 = 33$, $N_2 = 39$, $P = 0.22$). We conclude that most black-crowned recruits were probably yearlings, although some may have been floaters in a previous year. Brown-crowned recruits (57%, $N = 37$) were as likely to overproduce song as were black-crowned recruits (45%, $N = 47$, Fisher's exact test: $P = 0.38$).

Composition of Repertoires

Of the 49 recruits that overproduced song upon arrival, 34 (69%) sang two song types, 13 (27%) sang three types and two (4%) sang four types when first encountered. Males sang with near-immediate variety early in the season, repeating a song type four to five times before changing to another type. The recurrence interval increased in most males as one song type became increasingly favoured (see below). All but two of the overproducing recruits sang at least one version of the local dialect, dialect 1, in their repertoire. Thirty-four males (69%) sang two or more different versions, or song types, of dialect 1, differing primarily in the note complex (nine of these males sang three or four versions of dialect 1). In addition to dialect 1 in their overproduced repertoires, five males sang dialect 12, five males sang dialect 7, two males sang dialect 2, and one sang dialect 6 as the other dialect. Of the two males that did not sing a dialect 1 song, one male sang dialects 7 and 12, the neighbouring dialects to the north and south, respectively, and the other male sang two versions of dialect 2. Dialect 2 occurs north of dialect 7 from Newport, Oregon to Ilwaco, Washington, while dialect 6 is restricted to the Puget Sound area. Examples of overproduced repertoires are shown in Fig. 1.

Song Attrition

We had accurate data on the seasonal change in song type usage for 42 of 49 overproducing recruits. Thirty-four of the 42 males (81%) completed the attrition process and deleted all but one song type from their repertoires. The attrition process took a median of 9 days to complete (quartiles = 5.5, 13.5 days, range 2–60 days). Of the eight remaining males, two males that sang three or four song types early in the season discarded one or two types, but still retained two types for the remainder of our study. The other six males kept their initial two song types throughout their tenure in our study, up to four breeding seasons. To examine how males chose the final song for retention in their repertoires, in the next sections we examine note complexes and trills separately. Separate analyses are justified because in the 75 songs within the repertoires of the 34 males that completed the attrition process, the acoustic

structure of note complexes and trills varied independently. The acoustic similarity between the note complex and the most similar neighbour's note complex was uncorrelated with the acoustic similarity of the trill to the most similar neighbour's trill (Spearman's rank correlation: $r_s = 0.06$, $N = 75$ songs, $P = 0.59$). The $P_{critical}$ to control the false discovery rate at 0.05 for this and the next eight tests concerning song attrition was 0.022.

Attrition of Note Complexes

Of the 34 males that completed the attrition process, 25 (74%) retained the song containing the note complex that more closely resembled a neighbour's note complex (paired *t* test: $t_{33} = -3.031$, $P = 0.005$, 95% CI = −1.113, −0.204; Fig. 2). In 18 of 34 cases (53%), the neighbour with the most similar note complex was a returning adult, and across years, 60% of territory holders were returning adults. The mean similarity of the retained note complex to all neighbours' note complexes was also significantly higher than that of the deleted note complex(es) (Wilcoxon signed-ranks test: $T = 136$, $N = 34$, $P = 0.009$, 95% CI = −0.95, −0.145; Fig. 2). The two note complexes within the repertoires of males that overproduced were as different from one another as the retained note complex was from another note complex chosen at random from a non-neighbour in the population (paired *t* test: $t_{33} = -1.391$, $P = 0.17$, 95% CI = −0.726, 0.128; Fig. 3). In some cases, a male's two (or more) note complex types were clearly very similar and one could be considered to have been improvised from the other (e.g. male M-PiG in Fig. 1, whose two note complex types differed by a single terminal note). On average, however, the two or more note complexes within an overproduced repertoire appeared to have been learned from different tutor songs.

To examine whether overproduction followed by selective attrition increased a male's chances of matching a neighbour's note complex, we compared the minimum acoustic distance to neighbour songs for the retained song in recruits that completed the attrition process to the song in recruits that did not overproduce ($N = 54$). Note complexes retained by recruits that overproduced

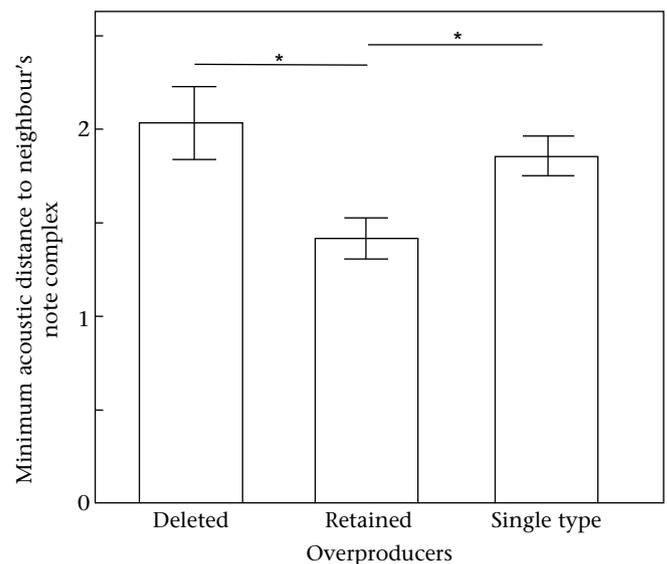


Figure 2. Minimum acoustic distances between note complexes in the songs of white-crowned sparrow recruits and their neighbours. Deleted and retained note complexes (on left) are the song types sung by the 34 males that completed the overproduction and attrition process. The rightmost bar depicts the note complexes in the repertoires of 54 recruits that did not overproduce. Means ± 1 SE are shown. Horizontal lines connect significantly different comparisons (see text).

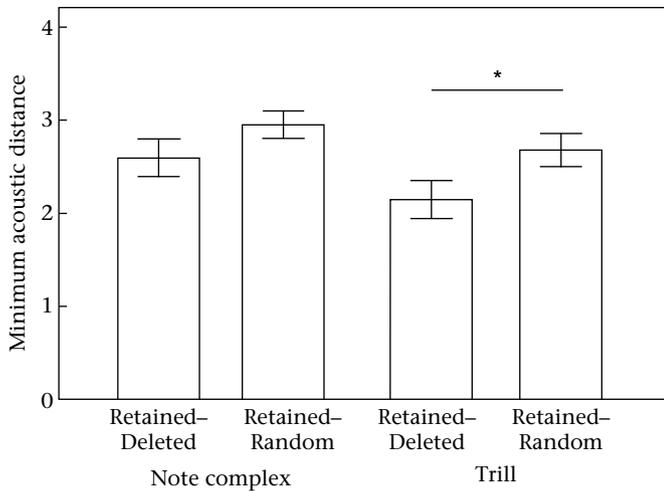


Figure 3. Minimum acoustic distances between retained and deleted phrases in repertoires of male white-crowned sparrows that overproduced ($N = 34$) compared to the minimum acoustic distance between the same phrase in the retained song and in one non-neighbour's song chosen at random ($N = 26$). Means \pm 1 SE are shown.

song upon arrival more closely resembled those of their neighbour upon completion of the attrition process than did note complexes of recruits that only sang a single song type initially (t test: $t_{86} = 2.77$, $P = 0.01$, 95% CI = 0.10, 0.96).

Attrition of Trills

Of the 34 males that completed the attrition process, two did not sing a trill in one of their overproduced song types, yielding $N = 32$ for trill comparisons. Twenty males (63%) retained the trill that more closely resembled a neighbour's trill, but, overall, retained and deleted trills did not differ significantly in their resemblance to a neighbour's trill (paired t test: $t_{31} = -0.806$, $P = 0.42$, 95% CI = -0.345 , 0.038). Mean acoustic distances to all neighbours also did not differ between retained and deleted trills (paired t test: $t_{31} = 0.43$, $P = 0.67$, 95% CI = -0.253 , 0.102). The 95% confidence intervals for the effect sizes associated with these negative findings were quite narrow (one-third of a standard deviation on the acoustic distance scale) and were centred on zero. Twenty-six of the 32 males sang two or more versions of dialect 1 trills, and so the differences between the trills in the birds' overproduced repertoires were often slight. In 20 of these 26 repertoires, spectrograms of the trills in the two or more song types appeared to be visually identical (e.g. song types A and B of males RG-M and M-PiG in Fig. 1), and the song types differed only in the note complex and sometimes (two males) the whistle and/or buzz. In six males (e.g. male LTH18 in Fig. 1), the trills differed between songs within the repertoire and so we assume the entire song types were learned from different tutors within dialect 1. The impression that trill variation was small within repertoires was borne out when we compared the acoustic distance between the two trills within each male's repertoire to the acoustic distance between the retained trill and a trill chosen at random from a non-neighbour. The two versions of dialect 1 trills in a male's repertoire were significantly more similar than were two randomly chosen dialect 1 trills (Wilcoxon signed-ranks test: $T = 61$, $N = 26$, $P = 0.003$, 95% CI = -0.815 , -0.279 ; Fig. 3). Six of the 32 males initially sang a dialect 1 song and at least one foreign dialect (e.g. RG-M in Fig. 1), and so had the option of matching or mismatching the dialect song by their neighbours. Of these, four retained the song with the trill that most closely matched a neighbour (binomial test: $P = 0.69$).

Song Sharing

In each of the 4 years, songs were distributed nonrandomly in the study area such that territory neighbours sang acoustically similar note complexes (Table 3). This would be the expected result of the selective attrition process described above. In contrast, there was no consistent tendency for neighbouring males to sing similar trills. In 2005 alone, males on neighbouring territories sang similar trills (Table 3).

Song Changes in Adulthood

In almost all cases, the attrition process in the bird's first breeding season resulted in a permanent reduction in the repertoire. However, we noted two exceptions to this rule. One male, WP-M overproduced two songs types in early April 2005 before discarding one type after 17 April. He returned each year from 2006 to 2008, and sang his original two types about equally often throughout all three seasons. Another male, M-OW was first captured in 2004, but did not hold a territory and sing until 2006. He overproduced at the beginning of both the 2006 and 2007 seasons before discarding the same song type each year. Such re-expression at the beginning of the singing season has been observed in the laboratory (Marler & Peters 1982b; Hough et al. 2000). The retained song type of male M-OW matched the dialect 7 song of the bird whose territory he was captured on as a floater in 2004 (and did not match any of his breeding neighbours). One final case of an apparent increase in repertoire size probably reflects inadequate sampling. M-PR sang one song type in 2005, a different type in 2006, and both types in 2007. No single 2007 recording ($N = 7$ different days) contained both song types. This male apparently repeated a given song type for a long time (>20 min) before switching, and we apparently missed single types in 2005 and 2006 given our sampling regime.

In the vast majority of cases, the structure of individual songs remained stable within and between years. Of the 261 males recorded multiple times within 1 year, and 108 cases where a banded male was recorded in 2 or more consecutive years, only two males made obvious modifications to a song type within or between seasons, but even then, the modifications consisted of deleting notes or borrowing notes from another song type in their repertoire. Yearling BR-M arrived on 18 April 2006 singing two song types. Over the next month, he modified one of these types by copying a note to the end of the note complex from the other note complex in his repertoire, and then apparently deleted notes from the same note complex so that it more closely resembled the note complex sung by two of his neighbours. He then modified this same note complex when first recorded in 2007 by adding a note to the

Table 3

Mantel tests for song sharing between neighbouring male white-crowned sparrows in 4 years

Year	Note complex r	P	Trill r	P
2005 ($N_i = 89$)	-0.044	0.0052*	-0.040	0.004*
2006 ($N = 80$)	-0.043	0.0118*	-0.003	0.844
2007 ($N = 79$)	-0.043	0.0120*	-0.010	0.490
2008 ($N = 90$)	-0.092	0.0002*	-0.016	0.234

The acoustic distances between note complexes and between trills are analysed separately. Negative Mantel r values in the body of the table indicate that birds sharing a territory border had acoustically similar phrases.

* Correlation was significant when the false discovery rate was 0.05 ($P_{critical} = 0.025$, $k = 8$ comparisons).

[†] N includes one retained song type for most males and all retained song types for those males (3–4 males/year) that retained two or more song types throughout the year.

end of the note complex. This latter addition made the note complex resemble his neighbours' note complexes even more closely (the same neighbours were present in 2006 and 2007). The second male, GP-M, sang a trill consisting of a series of dialect 1 notes, followed by dialect 7 notes in 2005. Such mixed trills are common further north at the border between these two dialects (Nelson et al. 2004). In 2006, he omitted the dialect 7 notes from the end of his trill. Two other males made minor changes by shortening the duration of a single note within their note complexes between years. Thus, after first arrival on the breeding grounds, white-crowned sparrow males alter their repertoire by deleting entire songs or parts thereof, but we have found no clear cases of the addition of novel notes or phrases to the repertoire.

DISCUSSION

Male Puget Sound white-crowned sparrows form a series of vocal dialects along the Pacific northwest coast of North America in which over 85% of males in local populations share the same terminal trill in their songs (Fig. 1). In contrast to this striking uniformity in the terminal trill, which is the result of accurate imitative learning (Nelson et al. 2004), the note complex in the song's introduction varies widely among males, and is used by males in individual recognition of neighbours (Nelson & Poesel 2007). In this study we found that the overproduction and attrition phase of the song-learning process had the effect of reducing this diversity in note complex structure in the local group of territory neighbours.

Over the course of this 4-year-long study, 51% of newly recruited male white-crowned sparrows overproduced song types upon their arrival on the breeding grounds in early spring. In most cases, the two or more song types in the repertoire had trills that matched the local dialect, dialect 1, but contained different note complexes. Males may sample a variety of tutors in their first summer and memorize the note complexes separately from trills, or else they may improvise their note complexes after learning from one tutor (see below). The fact that the vast majority of note complexes can be readily classified by humans into common 'types' (Baptista 1977; Nelson et al. 2004) suggests that males accurately memorize a variety of note complexes from different tutors, and improvise on a limited scale. The note complexes of song types within a repertoire were as different from one another as were two note complexes chosen at random from the population, creating the opportunity for the young male to choose one song with a note complex that differed from the note complexes in his neighbours' songs, or one that was shared as closely as possible, given his initial repertoire. Most of these males then proceeded to eliminate all but one song type from their repertoires, and preferentially retained the song type containing a note complex that more closely resembled the note complex in a neighbour's song. Rather than choose a song type that would increase their individual distinctiveness relative to their neighbours' songs, they chose the song type that resembled what their neighbours sang.

In contrast to the comparisons involving note complexes, we found no evidence that males chose their final song type based on acoustic similarity of their trill to the trills of their neighbours. This appears to be a consequence of the composition of the overproduced repertoire in young recruits: most song types within a male's repertoire had identical trills (Figs 1, 3), suggesting that they were learned the previous summer from one tutor, or perhaps were an average of several tutors' songs. As a result, there were no clear differences between trills that would afford males a basis for choice.

Our results thus suggest that song matching occurs over several spatial scales in different parts of white-crowned sparrow song.

Most males share the terminal trill over a 20–400 km stretch of coast, depending on the dialect (Nelson et al. 2004). Within our study population, in addition to sharing the trill, many males also converge on the same note complex, resulting in local neighbourhoods of shared note complexes.

Despite this close similarity in song structure, males are still able to discriminate between the songs of familiar neighbours and strangers (Nelson & Poesel 2007). In this experiment, neither the age of territory neighbours nor the acoustic similarity of their songs was controlled, and it remains to be seen whether sharing of note complexes by neighbours interferes with neighbour recognition. For example in the great tit, *Parus major*, McGregor (1989) found that unique song types of new territory neighbours were more readily discriminated than were shared song types. In contrast, shared song types are discriminable by banded wrens, *Thryothorus pleurostictus* (Molles & Vehrencamp 2001).

In white-crowned sparrows, males that overproduce and complete the selective attrition process are significantly more likely to match their neighbours' songs than are males that sing a single song type (Nelson 2000; this study). This is not the case in field sparrows (Nelson 1992). If song attrition produces sharing of note complexes in the local population, what maintains the co-existence of several note complex types within populations? We would expect the tendency to share note complex types to erode diversity in note complexes over time; however, the within-population variation in note complex types has not decreased over a 30-year period (Nelson et al. 2004). One possible explanation is that song sharing/not-sharing is a condition-dependent polymorphism, maintained in the population because each 'strategy' has advantages and disadvantages (Logue & Forstmeier 2008). Recruits that do not overproduce may be poorer learners (Nowicki et al. 2002) and perhaps sing with lower performance ability than overproducers. Note complexes are improvised at a higher rate than trills in wild populations and are imitated significantly less accurately than trills in a laboratory tutoring experiment (Nelson et al. 2004), perhaps because they are challenging to sing. Logue & Forstmeier's (2008) model predicts that lower-quality males may benefit by singing innovative songs, which may be difficult to compare to the songs of other males by eavesdroppers, while higher-quality males benefit by singing shared songs that can be easily compared. These speculations remain to be tested, although one prediction from Logue & Forstmeier's (2008) model, common also to a model positing that song matching is a conventional signal of aggression (Vehrencamp 2001), is met by our finding that males give stronger approach responses to playback of a shared song type than they do to a nonshared type (A. Poesel & D. A. Nelson, unpublished data).

Our results differ in one respect from a recent study on the song sparrow (Nordby et al. 2007) that also documented a tendency for males to prune their overproduced repertoires while selectively retaining matching song types. While the present study and a previous one on the same subspecies (Nelson 2000) found no tendency to modify the retained song type during the first singing season, young song sparrows (which have repertoires of 6–11 song types) modified about 25% of their songs from the early plastic song stage to become less similar to neighbour songs. The song sparrows in that study were resident, and were initially recorded in early plastic song in January and February. *Zonotrichia l. pugetensis* is still on the wintering grounds during this time, and most males arrive on the breeding grounds in late March and early April in a more advanced stage of song development. There is evidence in this and other species that an increase in circulating testosterone levels, stimulated in nature by the vernal increase in photoperiod, inhibits modification of song (Korsia & Bottjer 1991; Whaling et al. 1995). Male white-crowned sparrows might have to wait to modify their

songs until later in the year when testosterone levels decrease, but even then, they rarely do so.

The song-learning process in white-crowned sparrows, both the memorization of one or more tutor songs in the first summer, and the final selection of an adult song in the first breeding season, produces for many males conformity of the entire song with the songs of territory neighbours. An appreciable minority of males, however, do not share entire songs with their neighbours. The possible functional consequences of these differences in song sharing require study.

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References

- Baptista, L. F. 1977. Geographic variation in song and dialects of the Puget Sound white-crowned sparrow. *Condor*, **79**, 356–370.
- Beecher, M. D. 1989. Signalling systems for individual recognition: an information theory approach. *Animal Behaviour*, **38**, 248–261.
- Beecher, M. D., Nordby, J. C., Campbell, S. E., Burt, J. M., Hill, C. E. & O'Loughlin, A. L. 1997. What is the function of song learning in songbirds? In: *Perspectives in Ethology* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 77–97. New York: Plenum.
- Bell, D. A., Trail, P. W. & Baptista, L. F. 1998. Song learning and vocal tradition in Nuttall's white-crowned sparrows. *Animal Behaviour*, **55**, 939–956.
- Benjamini, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series C, Applied Statistics*, **57**, 289.
- Cunningham, M. A., Baker, M. C. & Boardman, T. J. 1987. Microgeographic song variation in the Nuttall's white-crowned sparrow. *Condor*, **89**, 261–275.
- Hough, G. E. II, Nelson, D. A. & Volman, S. F. 2000. Re-expression of songs deleted during development in the white-crowned sparrow. *Animal Behaviour*, **60**, 279–287.
- Korsia, S. & Bottjer, S. W. 1991. Chronic testosterone treatment impairs vocal learning in male zebra finches during a restricted period of development. *Journal of Neuroscience*, **11**, 2362–2371.
- Kroodsma, D. E., Baker, M. C., Baptista, L. F. & Petrinovich, L. 1984. Vocal "dialects" in Nuttall's white-crowned sparrow. *Current Ornithology*, **2**, 103–133.
- Lambrechts, M. M. & Dhondt, A. A. 1995. Individual voice discrimination in birds. In: *Current Ornithology* (Ed. by D. M. Powers), pp. 115–139. New York: Plenum.
- Liu, W.-C. & Nottebohm, F. 2007. A learning program that ensures prompt and versatile vocal imitation. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 20398–20403.
- Logue, D. M. & Forstmeier, W. 2008. Constrained performance in a communication network: implications for the function of song-type matching and for the evolution of multiple ornaments. *American Naturalist*, **172**, 34–41.
- McGregor, P. K. 1989. Pro-active memory interference in neighbour recognition by a songbird. *International Ornithological Congress*, **19**, 1391–1397.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**, 209–220.
- Marler, P. & Peters, S. 1981. Sparrows learn adult song and more from memory. *Science*, **213**, 780–782.
- Marler, P. & Peters, S. 1982a. Developmental overproduction and selective attrition: new processes in the epigenesis of birdsong. *Developmental Psychobiology*, **15**, 369–378.
- Marler, P. & Peters, S. 1982b. Structural changes in song ontogeny in the swamp sparrow *Melospiza georgiana*. *Auk*, **99**, 446–458.
- Marler, P. & Peters, S. 1982c. Subsong and plastic song: their role in the vocal learning process. In: *Acoustic Communication in Birds: II. Song Learning and Its Consequences* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 25–50. New York: Academic Press.
- Marler, P. & Tamura, M. 1962. Song "dialects" in three populations of white-crowned sparrows. *Condor*, **64**, 368–377.
- Molles, L. E. & Vehrencamp, S. L. 2001. Neighbour recognition by resident males in the banded wren, *Thryothorus pleurostictus*, a tropical songbird with high song type sharing. *Animal Behaviour*, **61**, 119–127.
- Morton, M. L. 2002. The mountain white-crowned sparrow: migration and reproduction at high altitude. *Studies in Avian Biology*, **24**, 1–236.
- Nakagawa, S. & Cuthill, I. C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, **82**, 591–605.
- Nelson, D. A. 1992. Song overproduction and selective attrition lead to song sharing in the field sparrow (*Spizella pusilla*). *Behavioral Ecology and Sociobiology*, **30**, 415–424.
- Nelson, D. A. 2000. Song overproduction, selective attrition, and vocal dialects in the white-crowned sparrow. *Animal Behaviour*, **60**, 887–898.
- Nelson, D. A. & Marler, P. 1994. Selection-based learning in bird song development. *Proceedings of the National Academy of Sciences U.S.A.*, **91**, 10498–10501.
- Nelson, D. A. & Poesel, A. 2007. Segregation of information in a complex acoustic signal: individual and dialect identity in white-crowned sparrow song. *Animal Behaviour*, **74**, 1073–1084.
- Nelson, D. A. & Soha, J. A. 2004a. Male and female white-crowned sparrows respond differently to geographic variation in song. *Behaviour*, **141**, 53–69.
- Nelson, D. A. & Soha, J. A. 2004b. Perception of geographical variation in song by male Puget Sound white-crowned sparrows, *Zonotrichia leucophrys pugetensis*. *Animal Behaviour*, **68**, 395–405.
- Nelson, D. A., Khanna, H. & Marler, P. 2001. Learning by instruction or selection: implications for patterns of geographic variation in bird song. *Behaviour*, **138**, 1137–1160.
- Nelson, D. A., Hallberg, K. I. & Soha, J. A. 2004. Cultural evolution of Puget Sound white-crowned sparrow song dialects. *Ethology*, **110**, 879–908.
- Nordby, J. C., Campbell, S. E. & Beecher, M. D. 2007. Selective attrition and individual song repertoire development in song sparrows. *Animal Behaviour*, **74**, 1413–1418.
- Nowicki, S., Searcy, W. A. & Peters, S. 2002. Brain development, song learning and mate choice in birds: a review and experimental test of the "nutritional stress hypothesis". *Journal of Comparative Physiology A*, **188**, 1003–1014.
- Podos, J. & Warren, P. S. 2007. The evolution of geographic variation in bird songs. *Advances in the Study of Behavior*, **37**, 403–458.
- Rohlf, F. 2000. *NTSYSpc User Guide*. Setauket, New York: Exeter Software.
- Slater, P. J. B. & Lachlan, R. 2003. Is innovation in bird song adaptive? In: *Animal Innovation* (Ed. by S. Reader & K. Laland), pp. 117–135. Oxford: Oxford University Press.
- Stoddard, P. K. 1996. Vocal recognition of neighbors by territorial passerines. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 356–374. Ithaca, New York: Comstock.
- Tibbetts, E. A. & Dale, J. 2007. Individual recognition: it is good to be different. *Trends in Ecology & Evolution*, **22**, 529–537.
- Trainer, J. M. 1983. Changes in song dialect distributions and microgeographic variation in song of white-crowned sparrows (*Zonotrichia leucophrys nuttalli*). *Auk*, **100**, 568–582.
- Vehrencamp, S. L. 2001. Is song-type matching a conventional signal of aggressive intentions? *Proceeding of the Royal Society Series B*, **268**, 1637–1642.
- Whaling, C. S., Nelson, D. A. & Marler, P. 1995. Testosterone-induced shortening of the storage phase of song development in birds interferes with vocal learning. *Developmental Psychobiology*, **28**, 367–376.