

# Urban noise and the cultural evolution of bird songs

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In urban environments, anthropogenic noise can interfere with animal communication. Here we study the influence of urban noise on the cultural evolution of bird songs. We studied three adjacent dialects of white-crowned sparrow songs over a 30-year time span. Urban noise, which is louder at low frequencies, increased during our study period and therefore should have created a selection pressure for songs with higher frequencies. We found that the minimum frequency of songs increased both within and between dialects during the 30-year time span. For example, the dialect with the highest minimum frequency is in the process of replacing another dialect that has lower frequency songs. Songs with the highest minimum frequency were favoured in this environment and should have the most effective transmission properties. We suggest that one mechanism that influences how dialects, and cultural traits in general, are selected and transmitted from one generation to the next is the dialect's ability to be effectively communicated in the local environment.

**Keywords:** cultural evolution; bird song; dialect; urban noise

## 1. INTRODUCTION

Cultural evolution can be described as the alteration or change in a learned behavioural trait from one generation to the next. Song dialects are a form of vocal geographical variation that develop in bird species that learn their songs, such as oscine passerines, and are one of the most extensively studied cultural systems in animals. Dialects arise when neighbouring populations have different song types and when the song variation between populations is greater than the variation within a population (Marler & Tamura 1962; Baptista 1975; Lemon 1975). Cultural transmission can perpetuate song dialects from one generation to the next when young birds learn local dialects from their parents and neighbours (Marler & Tamura 1964; Baptista 1977; Baptista & Petrinovich 1984, 1986; Baptista & Morton 1988; Petrinovich 1988*a,b*).

There is a wide range of temporal variation, from dialects that last for many generations to dialects that quickly arise and disappear (Podos & Warren 2007). For example, some species modify their songs in a year or less, such as the yellow-rumped cacique (Trainer 1989) and the indigo bunting (Payne *et al.* 1981). Other species, such as the rufous-collared sparrow (Handford 1981, 1988), chaffinch (Ince *et al.* 1980) and wood thrush (Whitney 1992), can maintain song dialects for decades or longer. However, the mechanisms that allow some dialects to go extinct and other dialects to be sustained are still unknown (Baker & Cunningham 1985; Catchpole & Slater 1995; Harbison *et al.* 1999). Bird song evolution is influenced by the mechanics of sound production (Nowicki *et al.* 1992; Podos & Nowicki

2004), environmental factors that affect signal transmission (Morton 1975; Wiley & Richards 1978; Ryan & Brenowitz 1985; Boncoraglio & Saino 2007), sexual selection (Searcy & Andersson 1986) and song learning (Slabbekoorn & Smith 2002). Presumably, the same factors that influence song evolution govern the cultural evolution of bird songs from one generation to the next.

One of the best-studied species with dialects is the white-crowned sparrow *Zonotrichia leucophrys* (Podos & Warren 2007). Considerable geographical variation exists in the structure of phrases, syllables and syntax in the songs of white-crowned sparrows, and, based on this variation, most songs of a region can be grouped into one or more dialects (Baptista 1975). Longitudinal studies of white-crowned sparrow song dialects demonstrate the longevity of dialects that are sung over large areas (18–30 years; Trainer 1983; Baker & Thompson 1985; Chilton & Lein 1996; Harbison *et al.* 1999), as well as the shorter lifespan of dialects that are sung in small areas (Chilton & Lein 1996; Harbison *et al.* 1999). Less permanent dialects are either modified or disappear and become extinct. One longitudinal study showed that the song structure (frequency and timing characteristics) changed with the changing vegetative structure over a 35-year period (Derryberry 2009).

To investigate the cultural evolution of bird songs over time and the mechanisms responsible for the cultural evolution of songs, we studied three adjacent dialects of the white-crowned sparrow over a 30-year time span. We compared the number of birds singing each dialect in recordings from urban San Francisco, California, in 1969/1970, in 1990 and in 1998. We also measured the minimum frequency of songs from each dialect in each time period. Baptista (1975) described three distinct

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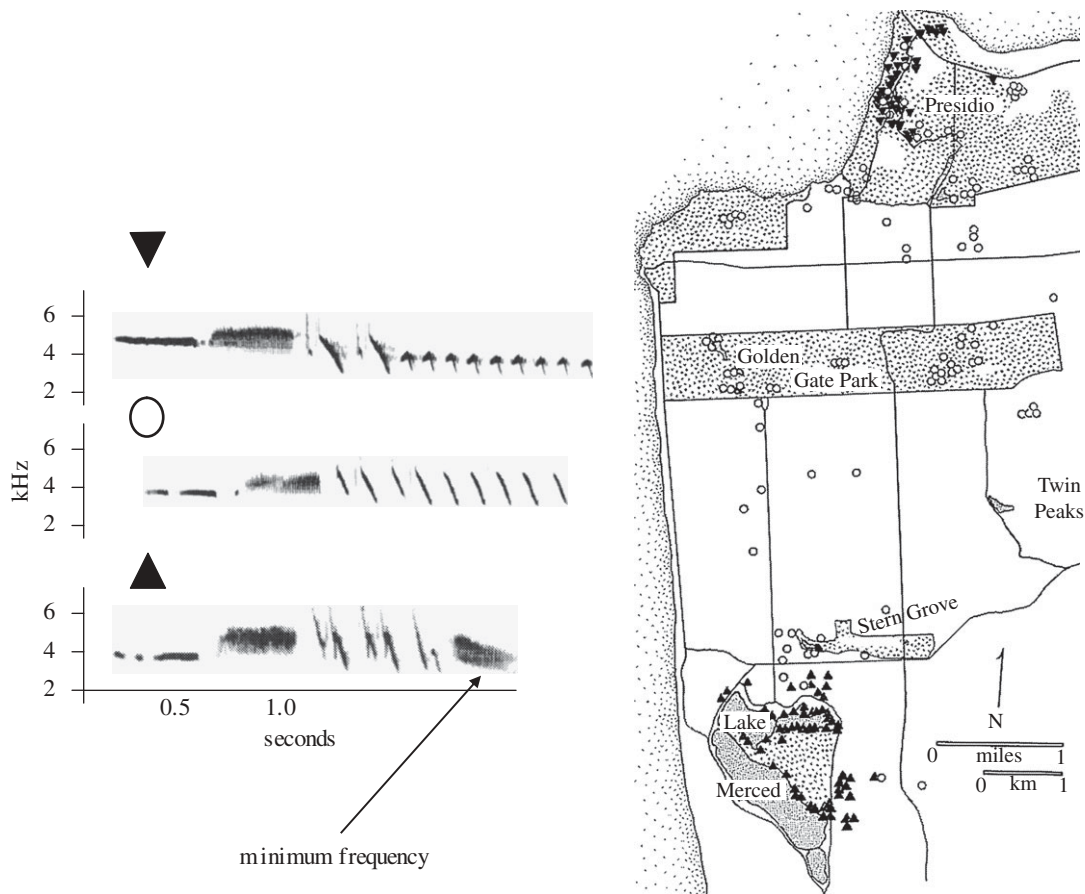


Figure 1. Map showing the three dialects in 1969 and 1970 in west San Francisco. The stippling represents vegetation while the white background represents concrete urban areas. Downward-pointing triangles are birds singing the Presidio (P) dialect, circles indicate the San Francisco (SF) dialect, and upward-pointing triangles indicate the Lake Merced (LM) dialect (Baptista 1975).

dialects of white-crowned sparrows *Zonotrichia leucophrys nuttalli* on the San Francisco peninsula in California: the Presidio (P), San Francisco (SF) and Lake Merced (LM) dialects (figure 1). Baptista (1975) observed that the SF dialect was spreading from interior urban San Francisco, which has higher amplitudes of ambient noise, into the LM and P dialect populations, where lower amplitudes of urban noise are found (Seto *et al.* 2007). Since our study took place in an urban setting, we hypothesize that if we find a difference in the minimum frequency over time, the lowest frequency of songs will shift to higher frequencies to avoid potential acoustic interference from the low frequency ambient noise of the urban acoustic environment (Slabbekoorn & Peet 2003; Patricelli & Blickley 2006; Wood & Yezerinac 2006). If the dialects are stable, we expect to find little or no difference between the abundance of each dialect over the 30 years of the study.

## 2. MATERIAL AND METHODS

### (a) *Study species and study sites*

The region of the P dialect consists mostly of west-facing slopes covered with moist chaparral, brushy areas at the edge of a golf course and gardens in residential areas. In 1969/1970, the P dialect was found throughout an area of approximately 1.6 km<sup>2</sup> with some interspersed birds singing the SF dialect. The Lake Merced region is also surrounded

by moist chaparral. In 1969/1970, the LM dialect was heard throughout an area of 2 km<sup>2</sup> with some birds of the SF dialect near the dialect boundary. In 1969/1970, birds singing the SF dialect were found in gardens, residential areas and parks throughout urban San Francisco and occupied an area of roughly 8 km<sup>2</sup> (Baptista 1975). Thus, the P and LM dialects were clustered in their respective habitats while the SF dialect was scattered throughout a larger area with no highly populated centre (figure 1). This difference might be explained by the fact that the P and LM dialects occur in regions with suitable habitat for dense concentrations of birds. Buildings and streets do not provide good habitat for white-crowned sparrows, but some of the urban gardens and parks provide suitable habitat for a few individuals and small groups of birds (Baptista 1975).

### (b) *Song recording*

In 1969/1970, Baptista recorded white-crowned sparrow songs in Presidio and at Lake Merced using an Uher 4000 Report-S tape recorder (tape speed 7.5 inches/s) and an Uher microphone mounted on a 24-inch parabolic reflector. Tapes were analysed on an Ampex tape recorder and a Kay Electric Company Model 6061A Sonograph with high-shape and wide-band settings (Baptista 1975).

In 1990, Baptista recorded white-crowned sparrows at Lake Merced in the same locations and with the same equipment as in 1969/1970. During the spring of 1998, Baptista and Luther recorded white-crowned sparrows throughout

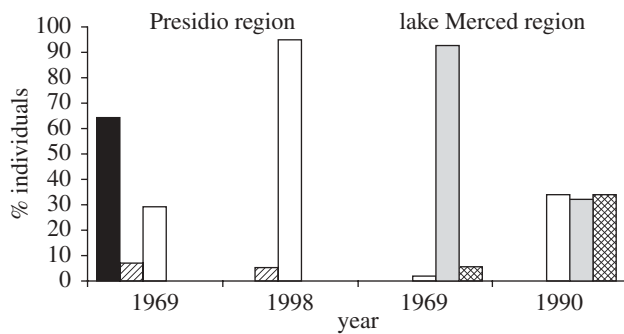


Figure 2. Percentage of individuals singing each dialect in the Presidio and Lake Merced regions of San Francisco in 1969/1970 and the 1990s. Black bar, P dialect; hatched bar, white bar, SF dialect; grey bar, LM dialect; cross-hatched bar, P/SF hybrid, LM/SF hybrid.

the Presidio region in an effort to find any that sang the P dialect. Songs were recorded with a Sony TC-D5 Pro II tape recorder and an Uher microphone mounted on a 24-inch parabolic reflector. Tapes were analysed with a Kay Elemetrics 5500 DSP Sonograph with a 300 Hz filter and an 8 kHz bandwidth.

### (c) Analysis

In the Presidio region, we recorded songs from 42 individuals in 1969/1970 and 65 individuals in 1998. Singing individuals were distinguished based on territory location. In the Lake Merced region, we recorded songs from 55 individuals in 1969/1970 and 53 individuals in 1990. The longest and clearest song recorded from each bird was selected for analysis. We detected three individuals that were bilingual (sang two different dialects). The bilingual individuals were removed before the analysis. We performed a qualitative and a quantitative analysis on all chosen songs to determine if dialects were stable and if the minimum frequency of each dialect changed over time.

We grouped songs into dialects based on visual characteristics obvious in the songs and Baptista's original description of each dialect (Baptista 1975). Songs were placed in the following groups: P, P/SF hybrid, SF, LM, LM/SF hybrid (figure 2). Hybrid songs combine syllables or phrases of two distinct dialects to create an intermediate song, and they are most common in birds that live on the boundaries between populations with distinct dialects (Baptista 1975; Baker & Cunningham 1985). We performed a Chi-squared goodness-of-fit test to determine whether the number of individuals singing each dialect had changed from 1969/1970 to 1990 or 1998 in the Lake Merced and Presidio regions, respectively.

We also analysed the minimum frequency of each song to determine whether there had been a change in the acoustic structure of the dialects over time. Using digital calipers, we measured the song's minimum frequency based on the lowest sound trace visible on the spectrograph. Our analysis focused on the minimum frequency, which is most likely to suffer acoustic interference from urban noise. We conducted a one-way analysis of variance (ANOVA) to test for a difference in the minimum frequency of each dialect in the earlier and later years of our study. We also used ANOVAs to compare the minimum frequency of songs between

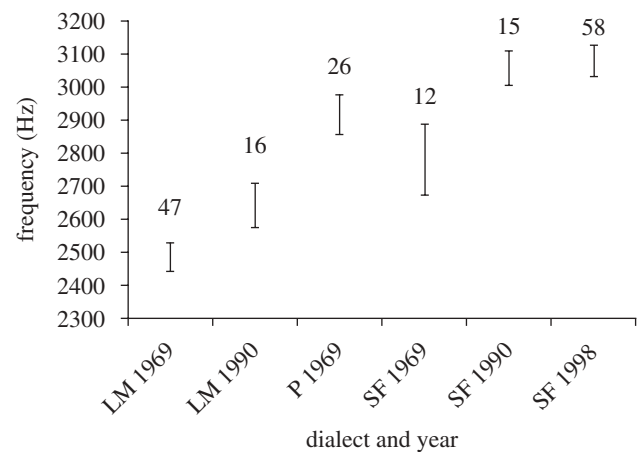


Figure 3. Minimum frequency of songs from each dialect and the year that they were recorded. The top and bottom bars indicate the s.e. of the Lake Merced (LM), Presidio, (P) and San Francisco (SF) dialects in 1969/1970, 1990 and 1998. The values above the bars indicate the sample size for each dialect and year.

dialects. All data were normally distributed (Shapiro–Wilk  $W$ -test  $p = 0.17$ ).

### 3. RESULTS

There was a large amount of turnover in the dialects sung by individuals in the Presidio and Lake Merced regions between 1969/1970 and the 1990s. In the Presidio, the P dialect went extinct, decreasing from 64 to 0 per cent between 1969/1970 and 1998, while the SF dialect increased from 29 to 95 per cent. The remaining birds sang P/SF hybrid songs. In the Lake Merced region, between the years of 1969/1970 and 1990 the number of individuals singing the LM dialect decreased from 93 to 32 per cent while the individuals singing the SF dialect increased from 2 to 34 per cent. The remaining birds sang LM/SF hybrid songs (figure 2). Chi-squared analysis revealed that the P and LM dialects were significantly less abundant and the SF dialect was significantly more abundant in 1998 and 1990 than in 1969/1970 ( $\chi^2 = 67.356$ , d.f. = 2,  $p < 0.001$ , and  $\chi^2 = 36.661$ , d.f. = 2,  $p < 0.001$ , respectively).

The minimum frequencies of the LM and SF dialects were lower in 1969/1970 than in the 1990s, while the P dialect could not be compared since it was extinct by 1998. One-way ANOVAs revealed that the minimum frequency of the SF dialect was significantly lower in 1969 ( $2780 \pm 106$  Hz) than in the 1990s ( $3077 \pm 48$  Hz;  $F_{1,68} = 7.48$ ,  $p = 0.013$ ). The minimum frequency of the LM dialect was also significantly lower in 1969/1970 ( $2469 \pm 41$  Hz) compared with 1990 ( $2640 \pm 70$  Hz;  $F_{1,61} = 4.41$ ,  $p = 0.040$ ; figure 3).

In 1969/1970 and the 1990s, the minimum frequency of the SF dialect was higher than that of the LM dialect and in 1969/1970 similar to the P dialect. The SF dialect was significantly higher than the LM dialect (the minimum frequencies in the SF dialect at Lake Merced =  $3045 \pm 71$  Hz and in the LM dialect =  $2523 \pm 35$  Hz;  $F_{1,78} = 43.35$ ,  $p < 0.001$ ). The P dialect ( $2914 \pm 60$  Hz) had a higher minimum frequency than the SF



dialect recorded in the Presidio region ( $2780 \pm 106$  Hz), although this difference was not statistically significant ( $F_{1,35} = 1.3$ ,  $p < 0.26$ ).

#### 4. DISCUSSION

Our results document the expansion of the SF dialect of the white-crowned sparrow, the extinction of the P dialect and diminished use of the LM dialect. The study also demonstrates that the minimum frequency of songs within the two remaining dialects of white-crowned sparrows in San Francisco have risen over the past 30 years. The SF dialect has replaced the P dialect and is in the process of replacing the LM dialect. In response to high levels of low-frequency ambient noise, urban birds have songs with higher minimum frequencies than rural birds (Slabbekoorn & Peet 2003; Patricelli & Blickley 2006; Wood & Yezerinac 2006). However, this is the first longitudinal study of urban bird songs to document a rise in the minimum frequency of songs over multiple generations.

Urban ambient noise might influence the cultural transmission of songs by favouring songs with higher minimum frequencies which should suffer less acoustic interference than songs with lower minimum frequencies (Lohr *et al.* 2003). Since white-crowned sparrows have a mean lifespan of 2 years with a longevity record of 13.3 years (Chilton *et al.* 1995), our recordings from the 1960s to 1990s could not include the same individuals. They thus reveal changes in songs transmitted across many generations of birds. Our results suggest that the influence of environmental factors on signal transmission can affect the cultural evolution of songs (Morton 1975; Wiley & Richards 1978, 1982).

Other longitudinal studies of white-crowned sparrow songs found that dialects in rural areas were relatively stable (Trainer 1983; Chilton & Lein 1996; Harbison *et al.* 1999). Some studies found shifts in dialect boundaries as a result of habitat alteration (Trainer 1983; Baker & Thompson 1985; Chilton & Lein 1996), but none of these studies observed shifts in the minimum frequencies of white-crowned sparrow songs.

One longitudinal study of white-crowned sparrow songs in rural habitat investigated quantitative changes in songs of white-crowned sparrows of the subspecies *pugetensis* and *oriantha* over a 35-year period (Derryberry 2009). In this study, shifts in the timing (the length of notes and time between notes) and frequencies of songs correlated with shifts in vegetation density over the same time period. Songs thus adapted to the changing vegetation in their local environment in a manner that provided optimal song transmission to intended receivers. Our finding that the lowest frequencies of urban white-crowned sparrow songs have risen over time likewise indicates that songs change to optimize transmission in the local acoustic environment. As anthropogenic ambient noise has increased in urban areas from the 1960s to the 1990s, especially due to more automobiles on the roads, songs with higher minimum frequencies should have a distinct advantage for cultural transmission.

One plausible explanation for the shifts to higher frequencies within dialects is that songs with higher frequencies were heard more clearly than other songs. Birds might only hear and learn parts of songs that were

not masked by ambient noise (Rabin & Green 2002). Since white-crowned sparrows continue to acquire songs for up to a year, they might learn songs that are best suited for transmission in the local acoustic environment of their breeding territories (Baptista & Morton 1988; DeWolfe *et al.* 1989). Alternatively, birds might learn multiple song templates but only retain and reproduce the one song best suited for transmission (Marler & Peters 1982). A third explanation could be that birds increase the frequency of their songs in response to louder noise, which was recently shown in house finches (Bermúdez-Cuamatzin *et al.* 2009).

Our results indicate an increase in the minimum frequency of songs of white-crowned sparrows in urban San Francisco over a 30-year time span. We suggest that the observed change occurred as a result of more efficient transmission of songs with higher frequencies in an urban environment. We propose that the local acoustic environment influences the cultural evolution of vocalizations like bird songs.

D.L. and L.B. began this project in 1998, while D.L. was a research assistant at the California Academy of Sciences. L.B. designed the study to document the extinction of the P dialect and provided recordings from 1969, 1970 and 1990. D.L. recorded songs in the Presidio in 1998. D.L. began the manuscript with L.B.'s help in 1999. L.B. died in 2000 and D.L. put the manuscript aside. In 2008, D.L. reanalysed the data and revised the manuscript to investigate the influence of urban noise on white-crowned sparrow songs. We would like to thank the California Academy of Sciences for logistical support. Amy Upgren, R. Haven Wiley and two anonymous reviewers provided help with early versions of this manuscript. Finally, D.L. would like to thank L.B. for introducing him to the fascinating study of bird songs.

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