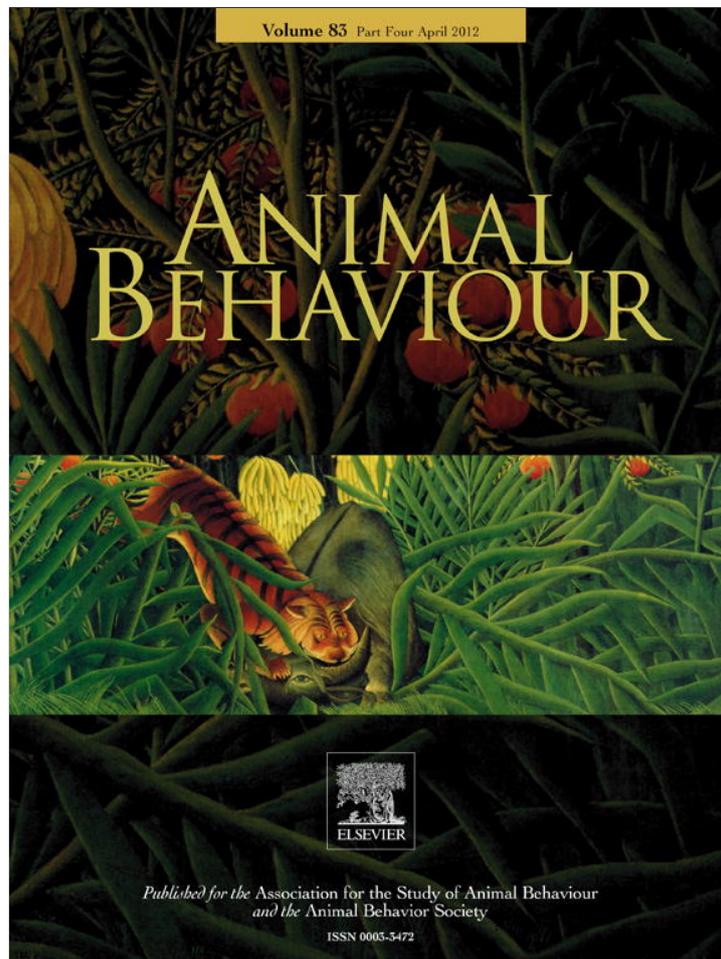


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Birdsongs keep pace with city life: changes in song over time in an urban songbird affects communication

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Animals in urban environments often must adjust their vocalizations to be heard over the din of anthropogenic ambient noise. Most studies of this process use current comparisons of environments that vary in ambient noise; here, we evaluate over time the effects of the urban environment on signal structure and salience. We show that white-crowned sparrow, *Zonotrichia leucophrys*, song increased in minimum frequency between 1969 and 2005 in San Francisco, California, U.S.A., coincident with rising levels of traffic noise. A higher minimum frequency is less likely to be masked by low-frequency ambient noise and thus is more likely to be effective as a communication signal. To test whether this change in song affects receiver response, we presented territorial males current (2005) and historical (1969) local songs. Males responded more strongly to current than to historical songs, suggesting that current songs communicate more effectively in the current local environment. The results suggest that behavioural adjustment to anthropogenic ambient noise over time can affect cultural evolution and communication. © 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Urban environments exert novel selection pressures on organisms, such as increases in noise pollution (Brumm 2004). Alteration of the ambient noise environment can affect the perception of acoustic mating signals and mask signal content (Patricelli & Blickley 2006; Slabbekoorn & den Boer-Visser 2006). Because acoustic communication is a critical component of both male–male competition and female mate choice in many taxa including anurans, crickets and birds (reviewed in Andersson 1994), the effects of urban ambient noise on signal transmission might have significant consequences for mate choice and resource defence across a diversity of taxa. Extensive research suggests that both anurans and birds adapt their vocalization behaviours to the urban acoustic environment (Brumm & Todt 2002; Slabbekoorn & Peet 2003; Brumm 2004; Wood & Yezerinac 2006; Parris et al. 2009; Pohl et al. 2009; Verzijden et al. 2010), and recent studies suggest that receivers respond to differences in signals between urban and nonurban areas (Mockford & Marshall 2009; Ripmeester et al. 2010). Most studies focus on current comparisons of environments that vary in ambient noise. Further insight into the effects of

the urban environment on signal structure and communication effectiveness could be gained by examining these processes over time.

Habitat-dependent selection is an important driver in the evolution of acoustic signals (Slabbekoorn & Smith 2002), and recent studies suggest that urban habitats also affect vocal behaviour (Slabbekoorn & den Boer-Visser 2006). In urban environments, anthropogenic noise, such as that produced by vehicles, tends to be loudest at low frequencies. Low-frequency ambient noise appears to have a significant effect on signal transmission, as acoustic signals vary in predictable ways between urban habitats and nonurban habitats. Studies conducted in cities around the world have noted that birds and amphibians in urban environments exhibit parallel behaviour in terms of altering their signals, by raising the minimum frequency of their vocalizations compared to the vocalizations of more rural populations (Slabbekoorn & Peet 2003; Fernández-Juricic et al. 2005; Patricelli & Blickley 2006; Slabbekoorn & den Boer-Visser 2006; Wood & Yezerinac 2006; Nemeth & Brumm 2009; Parris et al. 2009; Hu & Cardoso 2010). If acoustic signals also vary in predictable ways between periods with different levels of noise, then one interpretation is that signals are changing in response to changes in noise levels. Although it is debated whether an increase in minimum frequency is an effective adaptation to urban noise or the side effect of an increase in

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amplitude in response to urban noise (Nemeth & Brumm 2009, 2010), there is substantial evidence that a shift in minimum frequency is associated with increased ambient noise levels (Slabbekoorn & Peet 2003; Fernández-Juricic et al. 2005; Patricelli & Blickley 2006; Slabbekoorn & den Boer-Visser 2006; Wood & Yezerinac 2006; Nemeth & Brumm 2009; Parris et al. 2009; Hu & Cardoso 2010). Therefore, minimum frequency can be used as a measurable indicator of changes in signal structure in response to noise.

Changes in signal structure can affect signal content, and there is recent evidence that changes in vocalizations associated with urban habitats have functional consequences (Mockford & Marshall 2009; Ripmeester et al. 2010; Halfwerk et al. 2011a). Two of these studies suggest that song divergence between urban and nonurban areas affects male responsiveness, such that males from each area respond less to songs from the other area (Mockford & Marshall 2009; Ripmeester et al. 2010). The interpretation of these studies is that songs adapted to one environment are less effective communication signals in a different environment. A recent study also indicates functional consequences for male–female communication; in great tits, *Parus major*, high-frequency songs transmit better in noisy environments, but females prefer low-frequency songs (Halfwerk et al. 2011a). These studies provide important insight into the functional consequences of current levels of habitat-dependent signal variation. A more direct test of the effect of the urban environment on signal salience would be to measure the response of receivers to signals documented at different time points within a single population experiencing changes in ambient noise levels. A longitudinal design reduces the effect of other sources of variation that exist between distinct populations due to differences in the local environment and evolutionary history.

White-crowned sparrows, *Zonotrichia leucophrys*, are a particularly appropriate model organism for testing the effects of changes in signals and signal perception over time. White-crowned sparrow males typically learn to sing one song type that is shared among most males in a population (Chilton et al. 1995), and they sing this one song type with very little variation from one rendition to the next (Marler 1970; Baptista 1975). Variation in song within a population tends to be much less than that between populations, leading to a pattern of vocal geographical variation known as song dialects (Marler & Tamura 1962). Early interest in the function of song dialects in this species (Marler & Tamura 1962; Baptista 1975) resulted in a set of high-quality song recordings that spanned more than 30 years for many populations. Luther & Baptista (2010) compared songs from these older recordings to songs recorded more recently and documented an upward shift in minimum frequency in several dialect populations of white-crowned sparrows throughout San Francisco, California over a 30-year span. In this study, we examined changes in ambient noise levels and in song structure in San Francisco over a 36-year span, to test the hypothesis that cultural evolution of white-crowned sparrow songs in San Francisco is consistent with changes in urban noise levels over time. Second, we tested the hypothesis that changes in song structure over time have affected signal salience, by measuring the response of territorial white-crowned sparrow males to current (2005) and historical (1969) local songs in the Presidio Park in San Francisco.

METHODS

Study Population

In 1969 and 1970, Luis Baptista recorded singing white-crowned sparrow males in San Francisco from the Golden Gate Bridge in the Presidio south to Lake Merced and from the western edge of the

Golden Gate Park east to Twin Peaks (Baptista 1975) (see Fig. 1). In this area, he captured three dialects, 'Presidio', 'San Francisco' and 'Lake Merced'. The Presidio and Lake Merced dialects were generally contained within the park areas for which they were named whereas the San Francisco dialect spanned the entire area, including overlapping in range with the Presidio dialect in the Presidio. Luther & Baptista (2010) documented the disappearance of the Presidio dialect and a significant increase in the minimum frequency of the Lake Merced and San Francisco dialects. Here, we focus on the San Francisco dialect because (1) the geographical range of this dialect overlaps extensively with the geographical area for which we have current and historical measures of ambient urban noise levels (see Fig. 1) and (2) we have current and historical recordings of males singing the San Francisco dialect in the Presidio, thus reducing the effect of other sources of variation found in local versus foreign song comparisons.

Acoustic Analyses

Luis Baptista recorded songs in 1969 and 1970 using an Uher 4000 Report-S tape recorder (tape speed 7.5 inches/s (19 cm/s)) and an Uher microphone mounted on a 24-inch (61 cm) parabolic reflector. EPD made recordings in the Presidio in 2004 and 2005 using a Sony TCM-5000EV cassette recorder, a PRO-302 Unidirectional Dynamic microphone and a parabolic reflector. There were no consistent differences in sound quality between recordings made on these two sets of recording equipment (Derryberry 2007). There were also no consistent differences due to tape archival methods (Derryberry 2009). All songs were digitized with 16-bit precision at a 25 kHz sampling rate.

A previous study found a significant difference in the minimum frequency of the San Francisco dialect songs between 1969 and 1998 (Luther & Baptista 2010). In the present study, we evaluated differences in 18 temporal and frequency characteristics of the San Francisco song dialect between 1969 (eight birds) and 2005 (12 birds). We were unable to compare our measurements to those taken in the previous study because of differences in methodology and lack of access to the original recordings made in 1998. Thus, we compared songs between two rather than three points in time. For each song, we measured 18 parameters, including the duration (ms) and dominant, maximum and minimum frequencies (Hz) of the whole song and of each major section of the song (whistle, complex note and trill; see Results, Fig. 2) using Signal v3.1 (Beeman 1999). We measured dominant frequency as the frequency at which the most sound energy was transmitted during production of the relevant song section from a smoothed power spectrum (smoothing resolution 100 points). We also took minimum and maximum frequency measurements from smoothed power spectra at -36 dB relative to the peak amplitude frequency in the song. All other measurements were taken from digital spectrograms (256 point transform, frequency resolution = 97.7 Hz). We also calculated the frequency bandwidth (maximum–minimum frequencies) for each song section as well as the average note duration and rate of note delivery for the trill. Variables were log transformed and tested for significant differences in means between the two time points using two-sample *t* tests. We used Bonferroni correction to address the use of multiple comparisons (adjusted $\alpha = 0.003$).

Urban Noise

To evaluate changes in urban noise level over time in San Francisco, we compared the day-to-night noise level (L_{DN}) for 10 locations. The L_{DN} is the equivalent sound level in dB(A) for a 24 h

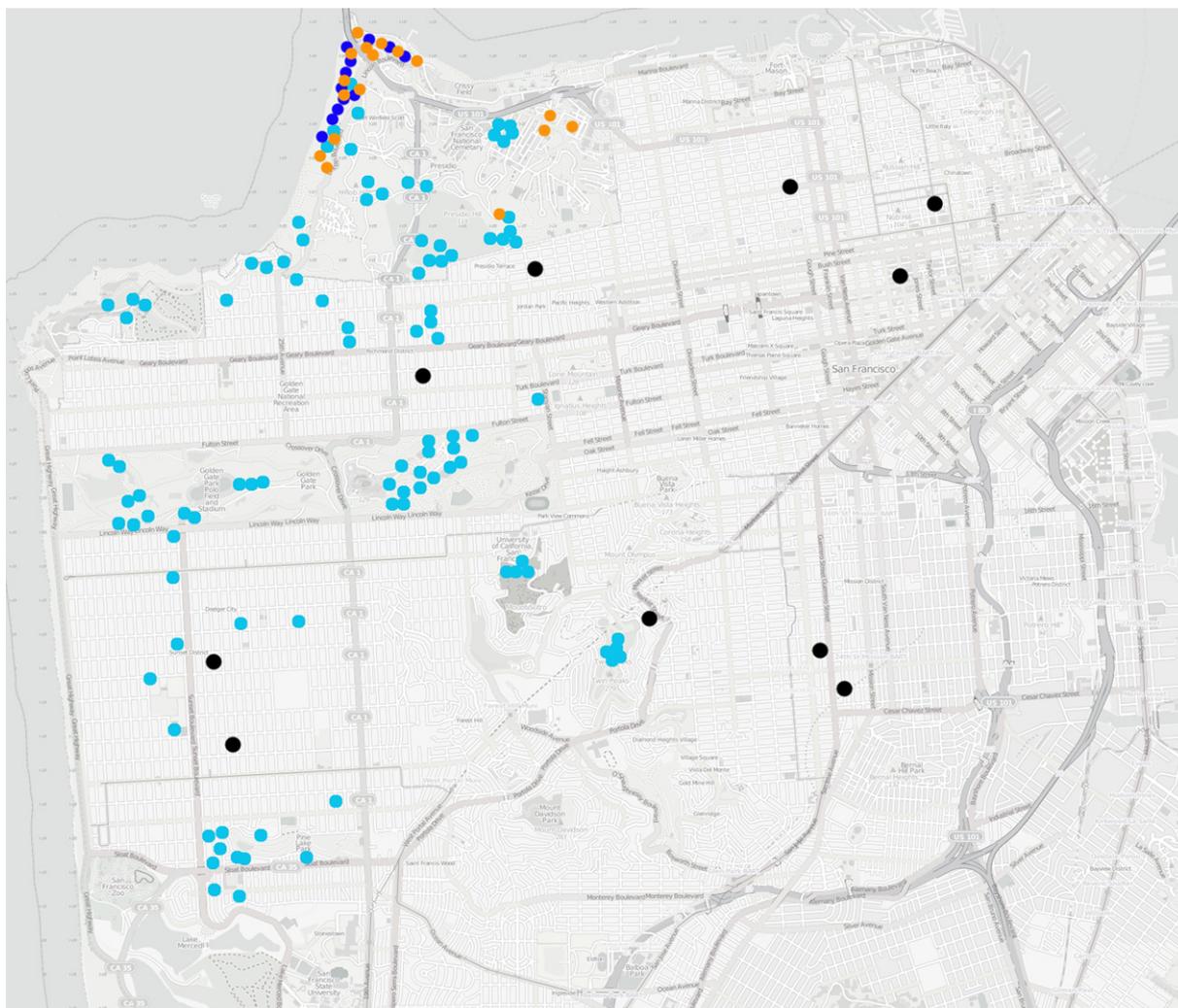


Figure 1. Map of San Francisco, CA, U.S.A. Black dots: the location of measurements of ambient noise in 1974 and 2008; light blue dots: sites where [Baptista \(1975\)](#) recorded territorial male white-crowned sparrows singing the San Francisco dialect in 1969; dark blue dots: sites where territorial males were recorded singing the San Francisco dialect in 2005; orange dots: locations of playback experiments.

period, but with an additional weighting of 10 dB imposed on night-time sounds. Using a noise measurement that reflects the overall changes in noise levels throughout the day and night is appropriate because it is unclear whether certain times of the day (e.g. dawn chorus) or noise levels throughout the day and night (e.g. increases in night singing in urban areas ([Miller 2006](#); [Fuller et al. 2007](#))) most affect avian singing behaviour. In 1974, the Environmental Protection Agency Office of Noise Abatement and Control measured L_{DN} at 11 sites distributed across the city ([Galloway et al. 1974](#)). For 10 of those sites, we were able to obtain values of L_{DN} estimated in 2008 by the [San Francisco Department of Public Health \(2008\)](#). We tested whether ambient noise level increased significantly between 1974 and 2008 using a Wilcoxon signed-ranks test. Of these sites, five occurred within the geographical range of the San Francisco dialect as examined by [Luther & Baptista \(2010\)](#) and two were close to the Presidio.

As the main source of traffic-generated noise in the Presidio is the Golden Gate Bridge, we also evaluated changes in the average number of vehicles using the bridge per day as collected by the [Golden Gate Bridge, Highway and Transportation District \(2010\)](#) for each year between the two time points for which we had recordings from white-crowned sparrows (1969 and 2005). Traffic flow is

a good approximation of traffic-generated noise and is routinely used to estimate outdoor noise levels in cities ([Seto et al. 2007](#)). However, if traffic volume becomes too high at any one point in time, noise levels can remain constant because vehicles moving at a slower rate generate less noise than vehicles moving quickly ([Halfwerk et al. 2011b](#)). We had no data on variation in vehicle speed on the Golden Gate Bridge, but we tested whether traffic flow changed over time using a linear regression model. Data were transformed to meet model expectations.

Playback Experiments

We selected five historical San Francisco songs from recordings made in 1969 and six current San Francisco songs from recordings made in 2005 in the Presidio ([Fig. 2](#)). We chose songs that had the least background noise but that also reflected the overall variation in the song type within the population at each time point. We presented songs to 20 territorial Presidio males singing the San Francisco dialect. For each playback experiment, we set the playback speaker, a RadioShack amplifier speaker, near the centre of a subject's territory, 2 m above the ground, connected with a 5 m lead to an iPod. After the speaker was in place, we selected

a playback song at random (iPod shuffle), subject to the constraints of the experimental design. Each of the 20 birds heard an historical song and a current song in a pairwise design. Historical and current song exemplars were played to a relatively equal number of birds. To test for any effect of pseudoreplication, we conducted a post hoc analysis to determine whether response varied significantly among song exemplars within each time point.

We conducted all playbacks between 0600 and 0900 hours. Playback trials began when the subject had been silent for at least 3 min. Each trial lasted 15 min (3 min before playback, 2 min of playback and 10 min afterwards). We conducted all playbacks to an individual within 1 m of the same location near the centre of its territory, separated treatments by at least 48 h to minimize habituation, and did not test territorial neighbours on the same day. Both trials had similar sound pressure levels as measured 1 min before playback. Each subject received treatments in a random order. All playbacks had the peak SPL adjusted to approximate that of natural songs (81 dB at 1 m, Realistic digital sound level meter, A weighting, fast response).

During the periods before, during and after each playback, we recorded (1) time from the start of playback to the first visible flight towards the speaker (latency of approach in min), (2) closest distance to the speaker (in m), (3) time from the start of playback to the first song (latency of song in min), (4) number of songs, (5) number of flights by the subject within 1 m of the speaker (6) number of wing waves. Low values for measures (1–3) and high values for (4–6) indicated strong responses to playback. A Bartlett's test of sphericity determined that the response variables were suitable for reduction (Mauchly test: $W \leq 0.001$, $\chi^2_{20} = 240.62$, $P = <0.001$). We used principal components analysis (PCA) to reduce the measures of response to a smaller number of independent variables. We used these independent response variables in signed-ranks *t* tests to compare individual responses to historical and current songs.

To test whether the amplitude of the background noise at a site affected the strength of response to current and historical songs, we ran a linear regression of these two variables. We subtracted PC1 and PC2 of responses to historical songs from responses to current songs for each bird. To test whether birds responded more strongly to current songs at louder sites, we included the difference in strength of response as the response variable and sound level (in dB) at sites as the determinant variable in a linear regression. We performed all statistical analyses using JMP 8.0 (SAS Institute, Cary, NC, U.S.A.) and the R statistical package (R Development Core Team 2008).

Ethical Note

Playback procedures adhered to institutional guidelines (Louisiana State University Institutional Animal Care and Use Committee Protocol 10-009) as well as to the legal requirements of the U.S.A.

RESULTS

Changes in Song over Time

Songs from the San Francisco dialect did not change in note type or note order between 1969 and 2005 (Fig. 2). Consistent with reported changes in songs between 1969 and 1998 (Luther & Baptista 2010), we found that the mean \pm SE minimum frequency of songs from 2005 was significantly higher (2806.13 ± 28.52 Hz, $N = 12$) than that of songs recorded from the same dialect in 1969 (2287.31 ± 42.37 Hz, $N = 8$; two-tailed *t* test: $t_{11,13} = -9.85$, $P = 7.85 \times 10^{-7}$). Of the 18 temporal and frequency characteristics compared between 1969 and 2005 (Table 1), we found five significant changes after correction for multiple comparisons. Of these

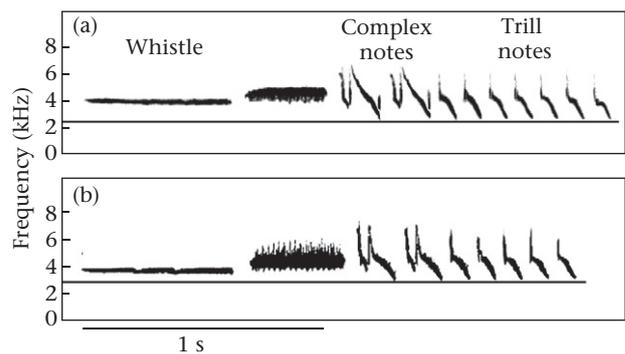


Figure 2. Sonagrams of San Francisco dialect songs of male white-crowned sparrows recorded in (a) 1969 and (b) 2005 in the Presidio. Major song sections (whistle, complex notes, trill notes) are indicated. The bottom horizontal line indicates the lowest frequency of each song.

five changes, four were increases in minimum or dominant frequency features (Table 1). The fifth change was a decrease in trill note duration, a change that is similar to differences in overall song duration found between urban and rural songs in other species (Bermudez-Cuamatzin et al. 2009; Francis et al. 2011a).

Changes in Urban Noise Level over Time

There was a significant increase in day-to-night (L_{DN}) noise levels at 10 sites in San Francisco between 1974 and 2008 (Mann–Whitney *U* test: $U = 2.5$, $N_1 = N_2 = 10$, $P = 0.013$; mean \pm SE L_{DN} : 1974: 66.13 ± 1.75 dB(A); 2008: 71 ± 2.38 dB(A); Table 2). An increase of 6 dB is double the sound pressure level. This result suggests that overall noise level increased in San Francisco between 1974 and 2008. We also evaluated vehicle counts from traffic toll data on the Golden Gate Bridge between 1969 and 2005 (Fig. 3). Between 1969 and 1989, there was a steady increase in the average number of vehicles per day (the maximum traffic flow in 1989 is the result of traffic rerouting after the 1989 earthquake). After 1989, traffic flow decreased, but the average number of vehicles in 2005 was still higher than in 1969 (representing an overall 19% increase). Overall, traffic flow significantly increased between 1969 and 2005 (linear regression: $R^2 = 0.48$, $N = 42$, $P = 1.56e-07$). In transportation noise models, an increase in traffic flow is correlated with an increase in traffic-generated ambient noise levels. Our findings suggest that traffic-generated noise in the Presidio from the Golden Gate Bridge increased between 1969 and 2005.

Response to Current and Historical Songs

All 20 males responded to both historical and current songs. PCA extracted two principal components (PCs) with eigenvalues greater than 1, which together explained 61% of the variation in response (Table 3). PC1 explained 37% of the variation and captured variation in movement behaviours (first flight, closest approach, number of flights and of wing waves). PC2 explained 24% of the variation and captured variation in singing behaviours (time to first song and number of songs). Positive values of PC1 and negative values of PC2 indicated a stronger response to playback. Males responded significantly more strongly to current song than to historical songs in both movement and singing behaviour (two-tailed *t* test: PC1: $t_{19} = -5.42$, $P = 0.001$; PC2: $t_{19} = -2.98$, $P = 0.007$; Fig. 4). Males responded to current songs more quickly and with more songs, and flew closer to the speaker, flew by the speaker more often and gave more wing waves than when they were presented historical songs (see Table 3 for individual behavioural responses).

Table 1
Results of statistical comparison of male white-crowned sparrow songs in San Francisco during 1969–2005 using two-sample *t* tests

Variable	Mean±SE		<i>t</i>	<i>P</i>
	1969	2005		
Song length	2141.54±71.12	1955.08±44.49	2.09	0.06
Whistle length	632.55±13.35	591.92±14.60	2.19	0.04
Complex length	177.19±4.83	168.47±5.15	1.36	0.19
Trill length	445.42±44.78	428.65±32.39	0.34	0.74
Trill note duration	85.30±1.54	78.97±1.46	3.10	0.006*
Trill rate	9.01±0.14	9.45±0.18	-2.06	0.05
Song maximum frequency	6345.89±162.64	6780.37±42.37	-2.32	0.04
Complex maximum frequency	6345.89±162.60	6772.10±85.93	-2.28	0.05
Trill maximum frequency	5830.58±267.33	6309.16±91.31	-1.70	0.13
Song minimum frequency	2287.31±42.37	2806.13±28.52	-9.85	7.8e-07*
Complex minimum frequency	2376.39±62.60	2820.48±30.85	-6.08	1.6e-04*
Trill minimum frequency	2371.20±37.07	2863.14±22.42	-10.8	4e-07*
Song frequency bandwidth	4058.58±180.94	3974.25±96.54	0.31	0.76
Complex frequency bandwidth	3969.50±184.32	3951.60±99.85	-0.01	0.99
Trill frequency bandwidth	3459.39±269.28	3446.02±88.46	-0.19	0.85
Whistle dominant frequency	3583.54±66.59	3815.41±66.66	-2.50	0.02
Complex dominant frequency	3514.84±143.13	4098.71±36.32	-3.96	0.005*
Trill dominant frequency	3651.12±109.38	4028.72±32.17	-3.33	0.01

Significant differences are indicated by an asterisk (Bonferroni corrected $\alpha = 0.003$).

We found no relationship between the ambient noise level during playback and male response behaviour (linear regression: PC1: $F_{1,18} = 1.8$, $R^2 = 0.1$, $P = 0.19$, power = 0.24; PC2: $F_{1,18} = 0.22$, $R^2 = 0.01$, $P = 0.65$, power = 0.07). We found no evidence of an effect of pseudoreplication. The song exemplars chosen to represent each time point did not significantly affect male response as measured by either PC1 (Kruskal–Wallis test: current songs: $H_5 = 3.8$, $P = 0.58$; historical songs: $H_4 = 2.7$, $P = 0.61$) or PC2 (Kruskal–Wallis test: current songs: $H_5 = 4.4$, $P = 0.50$; historical songs: $H_4 = 3.5$, $P = 0.48$).

DISCUSSION

The urban environment is expanding rapidly on a global scale and continues to impact the behavioural phenotype of many organisms. Many studies demonstrate that anthropogenic noise presents a problem for intraspecific communication and that birdsongs in urban areas differ from those in rural areas apparently to minimize communication errors caused by anthropogenic noise. By examining these processes over time, our study provides further insight into the effects of the urban environment on signal structure and salience. Comparing ambient noise levels across San Francisco, we found that anthropogenic noise has increased

significantly over the last 30 years. As predicted by an increase in noise levels, song dialects in San Francisco have increased in minimum frequency over this same period (Luther & Baptista 2010; this study). Taken together, these results suggest that songs have changed over time in response to increased anthropogenic noise in San Francisco. Consistent with the prediction of our second hypothesis, we found that male white-crowned sparrows gave stronger responses to current songs than to historical songs. This result suggests that historical songs are less effective at eliciting a response from intended receivers than current songs in the current context of territorial interactions. One interpretation of these results is that habitat-dependent selection on song (in the form of urban noise) affects both signal structure and signal salience. Our results align with previous studies on sensory pollution and suggest that cultural evolution of song can occur in

Table 2
Day-to-night (L_{DN}) noise levels at 10 sites in San Francisco during 1974–2008

Location	1974*	2008†
1818 Broadway (Arterial)	68.3	74
645 Leavenworth, No. 304: Arterial	75.2	79
1327 Guerrero St: Arterial	73.5	79
264 Fair Oaks: Local	61.9	74
1123 Clay, Apt 11: Arterial	69.5	74
1843 34th Ave: Local	60.5	64
2242 33rd Ave: Local	61.2	64
3873 Clay: Local	61.1	64
538 11th Ave: Local	61.9	59
10 Glendale: Local	68.2	79

* Source of 1974 measurements: Environmental Protection Agency Office (Galloway et al. 1974).

† Source of 2008 measurements: San Francisco Department of Public Health (2008).

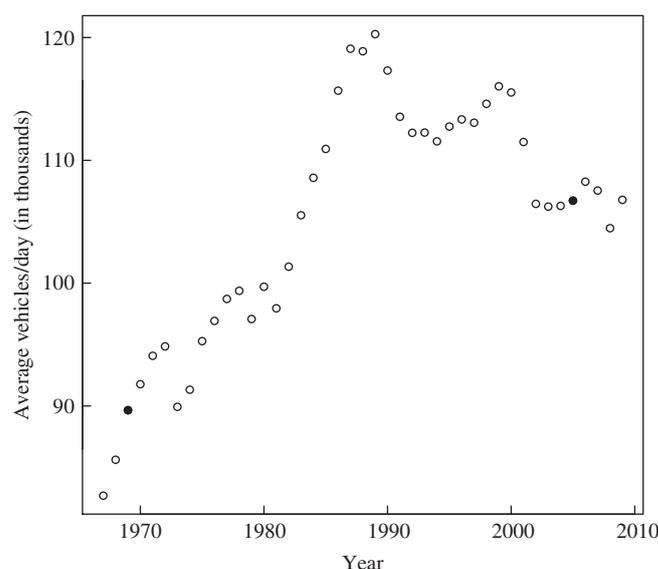


Figure 3. Scatterplot of the average number of vehicles crossing the Golden Gate Bridge, San Francisco, CA, U.S.A. per year between 1967 and 2009. Black dots indicate traffic flow for years when songs were recorded (1969 and 2005).

Table 3
Factor loadings for the first two principal components derived from behavioural responses to playback experiments

Response variables	PC1	PC2	Mean±SD	
			Historical songs	Current songs
First song (min)	−0.04	−0.69	0.67±0.54	0.35±0.29
Number of songs	0.2	0.68	12.67±5.02	19.05±6.24
First flight (min)	−0.49	0.09	4.91±7.56	0.91±0.97
Closest distance (m)	−0.51	0.18	3.13±2.30	2.28±1.67
Number of flybys	0.55	−0.11	0.67±0.91	2.05±1.68
Number of wing waves	0.4	0.09	0.24±0.77	1.21±1.51
Eigenvalues	37%	24%		

response to changes in urban noise levels, which subsequently affects signal salience. However, there are also competing hypotheses to explain our results, which we discuss below.

Our results are consistent with those of other studies that found differences in song between urban and rural populations. Most previous studies found that songs in urban populations tend to have higher minimum frequencies than songs in nonurban populations (Slabbekoorn & Peet 2003; Patricelli & Blickley 2006; Slabbekoorn & den Boer-Visser 2006; Wood & Yezerinac 2006; Nemeth & Brumm 2009; Hu & Cardoso 2010). In these studies, males were recorded in urban and nonurban areas and differences

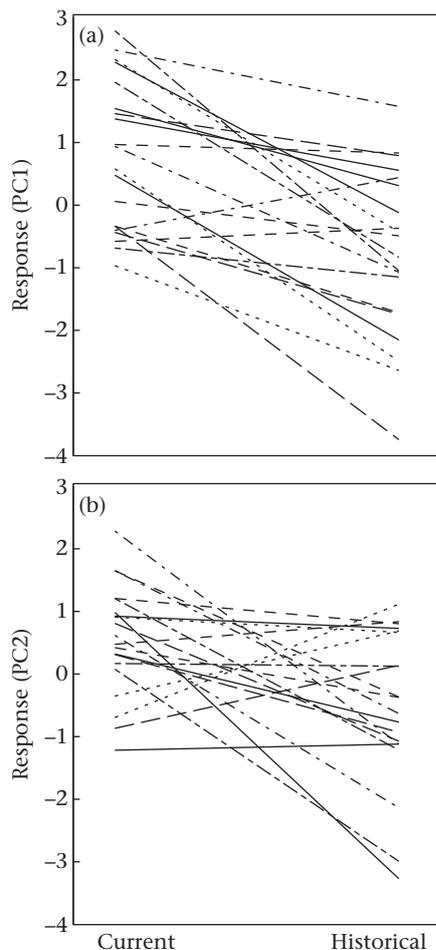


Figure 4. Paired result of male white-crowned sparrows' strength of response to historical and to current songs for principal components (a) PC1 and (b) PC2. Higher values of PC1 and PC2 reflect stronger responses to song. Each line represents the response of a different bird.

in song structure and ambient noise levels were assessed between the two populations. If differences were found in the predicted direction, then differences in song were assumed to be the result of differences in urban noise levels. Studies that have assessed songs of populations along a gradient of low-amplitude to high-amplitude ambient noise also found that birds at louder sites produce songs with higher minimum frequencies than birds at quieter sites (Parris & Schneider 2009; Francis et al. 2011a, b).

We also compared song structure and ambient noise levels, but over time rather than over space. Our results are also correlations, as we did not specifically test whether change in song structure is the direct result of changes in anthropogenic noise over time. However, studies of other populations of white-crowned sparrows have also provided a line of indirect support for habitat-dependent selection on song. White-crowned sparrow populations that have not been exposed to consistently loud levels of anthropogenic noise do not show an increase in the minimum frequency of their songs over time (Derryberry 2009). Instead, minimum frequency has decreased significantly over time in at least four rural populations of white-crowned sparrows in concordance with changes in their habitat (Derryberry 2009). Because these populations are experiencing changes in habitat, they are not perfect control populations for our study; however, taken together, these studies suggest that songs are changing in directions predicted by acoustic adaptation theory.

Note, however, that differences in historical and current song structure in the Presidio could be adaptive (i.e. an evolutionary response to selection or adaptive behavioural plasticity) or nonadaptive (i.e. cultural drift or a correlated response to behavioural plasticity; Patricelli & Blickley 2006). Next, we evaluate the adaptive and nonadaptive explanations for our results.

Experimental evidence on song perception and discrimination has shown that background noise in the frequency range of songs has the strongest effect on a birds' ability to discriminate between calls (Lohr et al. 2003), which supports the idea that changes in song are an adaptive response to avoid the masking effect of low-frequency background noise. Adaptive response to changes in the noise environment may occur via cultural evolution (change across cultural generations) or behavioural plasticity (change within individuals). One hypothesis states that songs may change across cultural generations in response to changes in habitat if juvenile males preferentially copy nonreverberated songs (i.e. cultural selection; Hansen 1979; Morton et al. 1986). If juvenile white-crowned sparrow males preferentially copy songs that are less masked by urban noise, then the change in song structure over time may be the result of cultural evolution.

Another adaptive mechanism is behavioural plasticity. Recent studies suggest that in some species, individual birds may be able to make short-term adjustments in their singing behaviour in response to changes in background noise (Bermudez-Cuamatzin et al. 2009; Halfwerk & Slabbekoorn 2009; Gross et al. 2010). For example, great tits select song types from their repertoire that are least masked by ambient noise (Halfwerk & Slabbekoorn 2009). Other species, such as house finches, *Carpodacus mexicanus*, appear able both to use different syllables and to modulate individual syllables (Bermudez-Cuamatzin et al. 2009). We do not know whether male white-crowned sparrows can also adjust the spectral characteristics of their song in response to changes in ambient noise levels; this is an empirical question.

We suggest, however, that cultural evolution is a better explanation than short-term behavioural plasticity of the patterns of song variation over time in San Francisco. As white-crowned sparrow songs were recorded at both time points without consideration of the background noise levels of territories, it is unlikely that all recordings in 1969 captured individuals singing at that moment a low-frequency version of their song type and that all

recordings in 2005 captured individuals preferentially singing a high-frequency version of the same song type. This scenario would have to occur in order for short-term behavioural adjustments to explain the pattern of song change found across 36 years. However, these two adaptive mechanisms are not mutually exclusive. It may be that white-crowned sparrow songs have changed over time because of cultural evolution in response to long-term changes in noise levels and that individual males may also adjust their songs to some extent in response to short-term changes in ambient noise levels.

An alternative interpretation of our results is that songs have evolved solely as a result of cultural drift. In the context of previous studies on song evolution it becomes apparent that drift alone is unlikely to explain the increase in minimum frequency over time. If changes in song structure are due to drift alone, then one would predict, on average, that an equal number of populations will increase, decrease or not change in minimum frequency over time. However, in at least nine populations (all rural) of white-crowned sparrows assessed to date, minimum frequency has either decreased significantly over time or not changed (Derryberry 2007, 2009, 2011, unpublished data). Only the dialects recorded in San Francisco have increased in minimum frequency over time. This pattern of results provides further support for the hypothesis that cultural drift alone cannot explain changes in song over time in the Presidio.

Another nonadaptive explanation for our findings is that the apparent increase in song minimum frequency is an epiphenomenon of increases in amplitude (Nemeth & Brumm 2009, 2010). This hypothesis suggests that birds sing louder when exposed to higher levels of background noise (i.e. via the Lombard effect), and that an increase in amplitude gives rise to a concomitant increase in frequency. Nemeth & Brumm (2009, 2010) found evidence that increases in minimum frequency were an indirect result of increases in song amplitude, suggesting that changes in minimum frequency are not an adaptive response to ambient noise levels. However, in a study on dark-eyed juncos, *Junco hyemalis*, Cardoso & Atwell (2011) found that louder singing does not explain an increase in minimum frequency in urban juncos. Instead, they suggested that juncos are able to adjust both song amplitude and frequency independently in response to changing noise levels or motivation. We were not able to test whether increases in minimum frequency over time result from increases in song amplitude, as accurate measurements of the amplitude of historical white-crowned sparrow songs are not possible. However, because adjustments in song amplitude are short-term responses to instantaneous changes in background noise, amplitude alone is unlikely to explain the long-term increase in song minimum frequency.

Our findings are also consistent with those of other studies that found differences in response behaviour between urban and rural populations. Two recent studies, one on great tits and one on European blackbirds, *Turdus merula*, found evidence that signal divergence between urban and nonurban areas affects male responsiveness (Mockford & Marshall 2009; Ripmeester et al. 2010). These studies provided the first evidence that vocal adaptation to urban environments could affect signal content in fitness-related communication contexts. Separating the effects of geographical variation on response (i.e. local versus foreign effects) from those of habitat-dependent selection was difficult in these studies. Ripmeester et al. (2010) controlled for local versus foreign effects in part by comparing male response to both high- and low-frequency rural and urban songs; however, other selective forces, such as sexual selection, could explain variation in response to current variation in frequency characteristics (Halfwerk et al. 2011a). Here, we examined responses to changes in songs over

time within one population; thus, males were exposed only to the local song type from their own habitat, controlling to a large extent for the effects of geographical variation. Similar to our study, Derryberry (2007) investigated the effect of habitat-dependent selection on songs over time. However, that study investigated the effects of changes in vegetation structure over time on signal salience whereas our current study investigated the effect of changes in ambient noise on signal salience at the same time as increases in noise pollution. Although Derryberry (2007) and the current study tested different hypotheses, in both cases the results suggest that habitat dependent-selection affects signal structure and receiver responses.

Although familiarity can affect response to songs (Milligan & Verner 1971; O'Loughlen & Beecher 1997, 1999), it is unlikely that a stronger response to current songs compared to historical songs can be explained solely by differences in familiarity (assuming that current songs may be more familiar because they more closely match the songs used in the current population). Individuals may give their strongest response to familiar songs and a proportionally lower response to unfamiliar songs depending on the degree to which these songs deviate from the standard (Shepard 1987). However, individuals have also been found to respond more strongly to novel (hence, unfamiliar) signals as well (Burley & Symanski 1998; Verzijden et al. 2007). White-crowned sparrows give stronger responses to local dialects as opposed to foreign dialects, but our experimental treatments were both from the same dialect, and, given the short life span of 1–2 years for white-crowned sparrows (Chilton et al. 1995), it is unlikely that individuals would previously have heard songs from either treatment. Thus, the unfamiliarity of historical songs did not necessarily predict that males would respond less to historical songs. The effects of familiarity and ambient noise are not mutually exclusive, but familiarity alone is unlikely to explain variation in response to these signals.

Our results suggest that males are most likely responding to changes in frequency characteristics of the San Francisco song over time. When we compared songs recorded in 2005 and in 1969, we found a large and significant increase in the minimum frequency of the complex note, the trill and the overall song, as well as in the dominant frequency of the complex note. Because these were the most dramatic changes in the song, we suggest that males were responding to these frequency differences between historical and current songs. However, we did not manipulate frequency characteristics, so males may be responding to other changes in song structure. For example, we found that an increase in minimum frequency is associated with a decrease in overall song length and in trill note length. A similar pattern has been found in other studies (Bermudez-Cuamatzin et al. 2009; Francis et al. 2011a), suggesting that there may be performance trade-offs between duration and frequency. Males may be responding in part to these trade-offs. Future research should attempt experiments with digitally synthesized songs for a more direct test of the effect of song minimum frequency on receiver responses in the presence of anthropogenic noise.

In conclusion, we provide evidence that ambient noise levels in San Francisco have gotten louder over time and that white-crowned sparrows have raised the minimum frequency of their songs over the same period. We also provide experimental evidence that male birds in urban environments give stronger responses to current songs than to historical songs. Based on acoustic theory, current songs with higher minimum frequencies increase their contrast with high levels of low-frequency anthropogenic noise more than do historical songs with lower minimum frequencies, and thus are more easily detected in the presence of anthropogenic noise. In addition, receivers are more likely to detect

salient content in signals that have reduced interference from local ambient noise. Signallers that fail to produce songs that receivers can detect correctly might have more difficulty establishing and defending a territory. Thus, there seem to be consequences to producing a song that is not adapted to local ambient noise levels in an urban population. It remains to be seen whether urban-dependent selection on songs also affects signal content in the context of female mate choice.

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