Behavioral Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2019), 30(6), 1734–1742. doi:10.1093/beheco/arz142

Original Article

Evidence for differing trajectories of songs in urban and rural populations

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Received 25 January 2019; revised 6 June 2019; editorial decision 3 July 2019; accepted 24 July 2019; Advance Access publication 19 August 2019.

INTRODUCTION

Animal signals adapt to local habitats to optimize transmission through the local habitats for increased signal efficacy; however, environments are always changing. In particular, environments face increasingly rapid and novel impacts from humans (Swaddle et al. 2015; Shannon et al. 2016). The local environment, both physical and acoustic, has a strong influence on the adaptations of song structure as songs must transmit through the vegetative structure (Wiley and Richards 1982) and be detected and discriminated in the presence of background noise (Wiley 1994). For example, birds can lower the frequency of their song in response to high-frequency insect noise (Slabbekoorn and Smith 2002; Tobias et al. 2010) or produce their songs at higher frequencies in the presence of relatively low-frequency anthropogenic noise, such as vehicular traffic (Slabbekoorn and Peet 2003; Shannon et al. 2016; Derryberry et al. 2016). Thus, the environment acts as a selective agent on songs, potentially driving changes in song in specific directions, but in many species, such as oscine passerine birds, because these songs are learned, they can also change over time via cultural processes, which can enable rapid shifts in song structure based on local conditions (Moseley et al. 2018).

Many animals exhibit cultural evolution, including humans (Henrich and McElreath 2003; Richerson and Boyd 2008), in a wide variety of behaviors such as foraging (Lachlan et al. 1998; Midford et al. 2000; Reader et al. 2003; Jaeggi et al. 2010), communicating (Parker et al. 2012), breeding (Danchin et al. 2004; Dall et al. 2005), and tool use (Whiten et al. 1999, 2005; Krützen et al. 2005). Although social learning and cultural evolution have been documented in a wide variety of taxa, there has been relatively

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little research into how changes in the local environment can affect the direction and rate of change of learned traits (but see Derryberry 2009). Because the environment is known to act as a selection pressure even on learned signals (Derryberry 2009), information on this front would drastically improve our understanding of social learning and cultural evolution. Generally, historical records of habitat type and changes to the environment are fairly easy to obtain, whereas detailed historical documentation of animal behavior is difficult to find or may not exist.

Our understanding of cultural evolution has been broadly informed by the study of animal communication signals, which have provided many of the details regarding how learned traits are passed from one generation to the next (Marler and Tamura 1962; Baptista 1975; Lemon 1975; Parker et al. 2012). In the case of imitative learning, young animals learn vocalizations from their parents, neighbors, or group members and then pass the learned trait on to the next generation (Marler and Tamura 1964; Baptista 1977; Petrinovich 1988; Ford 1991; Mennill et al. 2018). Long-distance communication signals, such as whale or bird songs, function in behaviors such as group cohesion, competition, and mate attraction, but these signals must also be transmitted through the environment and thus are shaped by both sexual and natural selection (Andersson 1994; Bradbury and Vehrencamp 2011).

Birds that alter the minimum frequency of their songs in the presence of anthropogenic noise also generally reduce the bandwidth of their song, which, unless matched with complementary increases in maximum frequencies, will, in turn, lead to a lower vocal performance capacity (Luther et al. 2015). Vocal performance is the ability to produce physically challenging songs, and birds that have a trilled component to their songs face limits such that they can either sing songs with rapid trill rates or have large frequency bandwidth, but are unable to maximize both (Podos 1997; Podos et al. 2009). The ability to produce and maximize both trill rate and bandwidth is important in male–male competition and female mate choice (Ballentine et al. 2004; Cramer and Price 2007; Illes et al. 2006; Moseley et al. 2013). Therefore, songs with reduced bandwidth receive weaker responses from territorial males than songs with greater bandwidth (Luther and Magnotti 2014) or with higher vocal performance (Luther et al. 2015; Phillips and Derryberry 2018).

Song complexity can also be important for sexual selection (Catchpole 1980; Searcy and Andersson 1986; Mountjoy and Lemon 1991; Catchpole and Slater 2003). Song complexity has been shown to correlate with brain space (Canady et al. 1984) and appears to be assessed as an honest signal of a singer's condition (Searcy and Yasukawa 1996; Spencer et al. 2005). Song complexity can take many forms from repertoire size to the variety of note types or the amount of frequency modulation within songs and notes (Catchpole and Slater 2003). In some species, the degree of frequency modulation within a syllable, as measured by the number of inflection points within a syllable (e.g., Podos et al. 2016), may be a potentially important signal of condition and fitness. This measure of syllable complexity has been evaluated to some extent in terms of species recognition (Nelson 1988, 1989; Luther 2009; Luther and Wiley 2009) but has not been investigated in the context of song performance.

We propose the idea that in situations where vocal performance based on trill rate and bandwidth is diminished, syllable complexity might instead be enhanced, thus serving as a different axis through which individuals could reveal their quality. For example, in swamp sparrows (SWSP), *Melospiza georgiana*, the larger bill of the coastal swamp sparrow subspecies, *Melospiza georgiana nigrescens*, is associated with differences in song structure compared with inland males (Liu et al. 2008), which have led to reduced vocal performance in the songs of coastal males, as the larger bill inhibits them from opening and shutting the bill as widely and quickly as inland birds with smaller bills, which results in lower bandwidth or slower trill rates, or both (Ballentine 2006). Male and female SWSP discriminate between songs of the coastal and inland subspecies and prefer their own song types (Ballentine et al. 2013). Although the coastal SWSP have lower vocal performance, their songs have become more complex in terms of note structure and variety, which appears to be a more salient trait in receivers in coastal populations (Ballentine 2006; Ballentine et al. 2013).

Here we examine changes in a culturally evolved trait, birdsong, over nearly 50 years. We use a database of nearly 1300 songs recorded during 2 time periods—historical 1968–1972 recordings by Luis Baptista and contemporary 2012–2016 recordings. We focus on 2 main features in the songs of white-crowned sparrows (WCSP; *Zonotrichia leucophrys nuttalli*): the complex syllable and the simple trill (Figure 1), which are associated with mate attraction, territorial, and defense and assessed for vocal performance (*nuttalli* subspecies Luther et al. 2015; Phillips and Derryberry 2017). We hypothesize that anthropogenic noise affects the process of cultural evolution of WCSP song, such that male birds exposed to consistent low-frequency

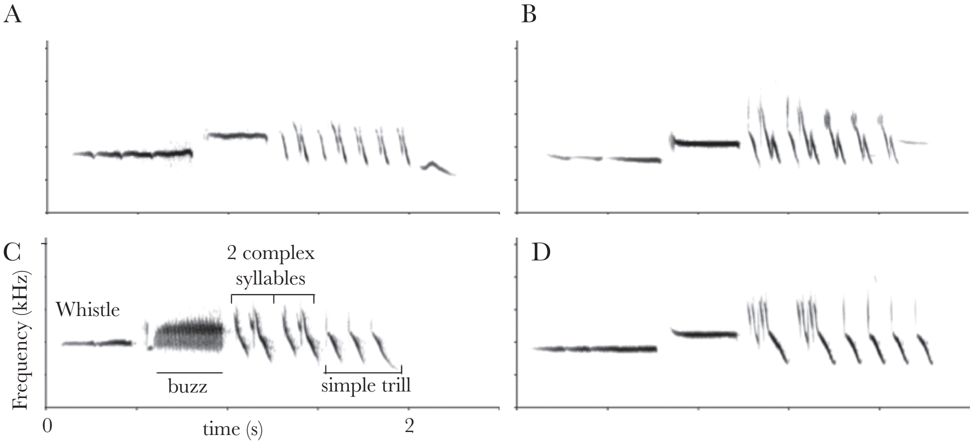

Figure 1

Four example song spectrograms of the white-crowned sparrow (WCSP) from rural populations (top a, b) and urban (bottom c, d)—historical (left a, c) and contemporary (right b, d) recordings. WCSP song consists of an opening whistle followed by a buzz or buzzy whistle, the complex syllable(s), and then the simple trill.

anthropogenic noise, such as those in urban areas will have different trajectories over time than birds that are not exposed to as much anthropogenic noise. Indeed, many aspects of urbanization in addition to anthropogenic noise may affect wildlife populations; however, recent studies have shown a significant increase in anthropogenic noise in urban areas in San Francisco, which is likely to greatly affect animals that communicate acoustically (Luther and Derryberry 2012).

Based on our previous findings that WCSP songs are more limited in bandwidth in populations with greater exposure to anthropogenic noise when compared with populations with less exposure (Luther and Derryberry 2012; Derryberry et al. 2016), we predict a decrease in vocal performance over time, but an increase in vocal complexity in populations with greater exposure to anthropogenic noise. We hypothesize that increased complexity would be a different trait through which to advertise performance. We also compare changes over time for songs from populations of birds with less exposure to anthropogenic noise, such as those in rural areas, because we do not have reason to predict a directional change in song complexity or vocal performance over time.

METHODS

The WCSP is a year-round resident in coastal central California and a classic study organism with a long history of research on its song and behavior, especially the populations that occur in and around San Francisco, CA (Baptista 1975; Petrinovich and Patterson 1982; Baker and Cunningham 1985; Dewolfe et al. 1989; Luther and Baptista 2010; Derryberry et al. 2016). To examine our predictions, we used songs recorded between 1968 and 2016 from free-living WCSP males identified by their territory locations (historical) and males in the mid-2010s, the majority of which were uniquely color-banded throughout San Francisco, CA (urban) and nearby (<50 km) Marin County (rural). Birds in the urban and rural locations comprised several subpopulations with varying levels of anthropogenic noise and other environmental stimuli. We focused on 3 dialects for which we had a good representation of both contemporary and historical song recordings: the San Francisco dialect (urban) (Baptista 1975), Clear dialect (rural), and Drake dialect (rural) (Baker and Thompson 1985). A portion of this dataset has been used in other studies (rural-historical songs (Derryberry 2009); contemporary urban songs (Derryberry et al. 2016); here, we include additional recordings and locations as well as measurements from different song components.

Because recordings represent time points separated by nearly 50 years, different individuals and recording devices were used to make recordings. Between 1968 and 1972, Luis Baptista recorded WCSP songs throughout Marin County and the city of San Francisco with an Uber 4000 Report-S tape recorder with a tape speed of 7.5 inches/s and an Uber Microphone mounted on a 24-inch parabolic reflector. We digitized his recordings as WAV files with 16-bit precision at a 25-kHz sampling rate using Syrinx 2.2b and an Echo Digital Audio sound card (Derryberry 2009). Between the years 2002 and 2016, we made recordings using a Sennheiser ME62 omnidirectional microphone mounted on a Saul Mineroff PR-1000 parabola and a Marantz PMD 661 MKII digital recorder set at 44.1 kHz sampling rate, 16-bit, and WAV file type (Derryberry et al. 2016). All songs were recorded during the breeding season between April and July. In previous articles, we demonstrate that differences in recording devices and storage of the historical recordings do not have a significant effect on temporal and spectral features of the songs (Derryberry 2007).

High-quality songs were chosen for analysis by acoustic and visual inspection of spectrograms in the sound analysis software program Raven v1.5 (Bioacoustics Research Program, Cornell Laboratory of Ornithology 2012) along a frequency range between 0 and 11.025 kHz (Nyquist frequency). The selected songs were saved as individual WAV files and normalized in Audacity to −1 dB. Songs were high-pass filtered at 1500 Hz to eliminate noise below the frequency range of WCSP song. We took measurements using a Hann window with a window size of 680 samples (0.0154 s) per a 3 dB filter bandwidth at 93.3 Hz. Window overlap was 50%, hop size 340 samples (0.00771 s), and the discrete Fourier transformation size was 1024 samples with Grid spacing of 43.1 Hz.

We collected 2 sets of data from our recordings, each based on a different song phrase type. All WCSP songs begin with a whistle, followed by a series of other phrase types, and usually end in a simple trill. All dialects in our study contained a complex syllable, which is a sequence of unrepeated notes, typically found in the first half of the song. In some cases, this syllable was repeated, but to standardize our measurements, we only measured acoustic features of the first complex syllable. All 3 dialects also contained a series of repeated simple syllables or notes at the end of the song, often referred to as the trill. From the trill, we measured the trill rate and bandwidth to calculate a measure of vocal performance referred to as vocal deviation as described below (Podos 1997).

For the complexity dataset, we took measurements on the first complex syllable in a song as individuals and dialects vary in the number of syllable complexes. We used the Peak Frequency Contour (PFC) tool, which traces signals according to the points of peak energy along the contour (see Charif et al. 2010 for further details). Song measurements included 90% duration, PFC minimum frequency, and PFC maximum frequency of the normalized syllables. We calculated syllable bandwidth by subtracting the PFC minimum frequency from the PFC maximum frequency for each syllable. Complexity was measured as the number of changes in inflection, that is, changes in frequency direction (Luther 2009). We measured complex syllables from a total of 1297 songs from 209 individual males (see Table 1).

For the vocal performance dataset, we took measurements on the terminal trill following methods in Podos (1997). We calculated trill rate (Hz) as the number of notes per second. We then calculated frequency bandwidth as the difference between the maximum and minimum frequencies from a reference of −36 dB. Using the morphological limit described for 34 species of sparrows $-y = -0.124 + 7.55$ (Podos 1997), we calculated the orthogonal distance of each song from this upper bound, which is known as the vocal deviation. Vocal deviation estimates the extent to which a bird maximizes trill rate at a given bandwidth for a specific song (Wilson et al. 2014). We measured vocal deviation for 1138 songs from 281 males (Table 1).

For both questions of complexity and vocal performance, we first averaged all sound analysis measurements by individual males for the over 1200 songs (Table 1) and used means per male in the following analyses. To determine whether song performance and complexity differed more between habitat type or time period than within each, we ran generalized linear models in R (r-project.org) with a Gaussian distribution. This test modeled the effects on song measurements of habitat type (urban/rural), time (contemporary/historical), and an interaction term (habitat by time), indicating how the combination of urbanization and changes over time might affect differences in performance and complexity. The GLM in R provides *P* values for Anova tests and *F*-tests.

Table 1

Sample sizes of males and songs used for analysis of syllable complexity and vocal performance

Habitat	Time	*N* males	Songs per male	Average songs per male	Total songs
Complexity					
Rural	Current	89	1-36	8.1	720
Rural	Historical	35	1-10	2.3	81
Urban	Current	24	1-11	4.3	104
Urban	Historical	61	1-14	6.4	392
Performance					
Rural	Current	50	1-18	7.3	363
Rural	Historical	94	1-10	1.6	147
Urban	Current	89	1-18	6.3	565
Urban	Historical	48	1-2	1.3	63

Table 2

Complexity, the number of inflection points in the first complex syllable, varied significantly by habitat and over time, whereas the bandwidth was not different between habitats but was different over time

	Estimate	Standard error	T	*P* value
Duration complex syllable				
(Intercept)	0.092	0.015	6.26	2.24E-09***
Habitat	0.054	0.011	5.14	6.42E-07***
Time	0.040	0.012	3.35	0.000965***
Habitat × time interaction	0.043	0.016	2.79	0.005736**
Bandwidth complex syllable				
(Intercept)	3490.0	116.0	30.09	2.00E-16***
Habitat	25.3	83.6	0.30	0.762
Time	−614.8	95.0	−6.48	6.90E-10***
Habitat × time interaction	−136.1	123.3	−1.10	0.271
Number of inflection points				
(Intercept)	12.75	0.95	13.37	2.00E-16***
Habitat	−1.57	0.69	−2.29	0.0233*
Time	−2.02	0.78	−2.59	0.0104*
Habitat × time interaction	−0.79	1.01	−0.78	0.4386

Complex syllable duration significantly differed between habitats and over time as well as the interaction between the 2 variables. Tests were regarded as statistically significant at $\alpha = 0.05$.

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

RESULTS

Complexity

Complex syllables changed significantly over time, and the extent of change varied among urban and rural habitats (Table 2, Figure 2 top row). The duration of the complex syllable differed significantly across urban and rural habitats as well as across time periods, but there was no significant interaction between these 2 terms. Specifically, the duration of the complex syllable decreased considerably for urban songs from historical to contemporary time periods. We also found that the bandwidth of the complex syllable increased over time, and the degree of change was similar in both urban and rural habitats. Complexity, as measured by the number of inflection points in the complex syllable, significantly increased over time and differed between urban and rural habitats. Urban songs exhibited a greater increase in complexity over time, but the interaction between habitat and time was not significant.

Vocal performance

Vocal performance of the simple trill also differed across habitats and time (Table 3, Figure 2 bottom row). Over time, trill rate decreased and bandwidth increased significantly for songs in both rural and urban habitats. The effect sizes of change over time differed between habitats with smaller decreases in trill rate and significantly greater increases in bandwidth for urban songs (Table 3). Combined, these changes in song traits resulted in vocal deviation differing across time and habitats, with a significant interaction between time and habitat, such that contemporary urban songs had the highest vocal performance (lowest vocal deviation) for the simple trilled portion of the song.

Minimum frequency

Despite the result that bandwidth of both the complex syllable and the simple trill portions of the songs increased over time for urban songs, the minimum frequency of the whole song shifted up significantly by an average of 327.8 ± 110.4 Hz (GLM $t = -2.968$, $P = 0.007$) in urban habitats, which is consistent with previous findings of acoustic adaptation to urban noise in this system (Luther and Baptista 2010; Luther and Derryberry 2012; Derryberry et al. 2016).

DISCUSSION

There is a strong yet still growing literature on the modification of animal vocalizations in the presence of anthropogenic noise, yet few have investigated the trajectory or implications of these changes

Table 3

The note repetition rate of the trill was significantly different between habitats and over time

	Estimate	Standard error	*T*	*P* value
Sig.				
Trill rate (intercept)	7.9474	0.2775	28.635	<2.00E-16***
Habitat	0.9043	0.2383	3.796	0.000181***
Time	0.9531	0.2405	3.963	9.43E-05***
Habitat × time interaction	−0.1083	0.3363	−0.322	0.747687
Trill bandwidth				
(Intercept)	3840.25	103.38	37.146	<2.00E-16***
Habitat	−250.00	88.75	−2.817	0.0052**
Time	−709.13	89.59	−7.916	5.96E-14***
Habitat × time interaction	−505.38	125.27	−4.034	7.09E-05***
Vocal deviation				
(Intercept)	21.3378	0.9229	23.120	2.00E-16***
Habitat	1.7431	0.7923	2.200	0.0286*
Time	4.4313	0.7997	5.541	7.00E-08***
Habitat × time interaction	4.5240	1.1183	4.045	6.78E-05***

The bandwidth and vocal deviation of the trill were significantly different between habitats, over time, and the interaction between habitat and time. Tests were regarded as statistically significant at α = 0.05.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

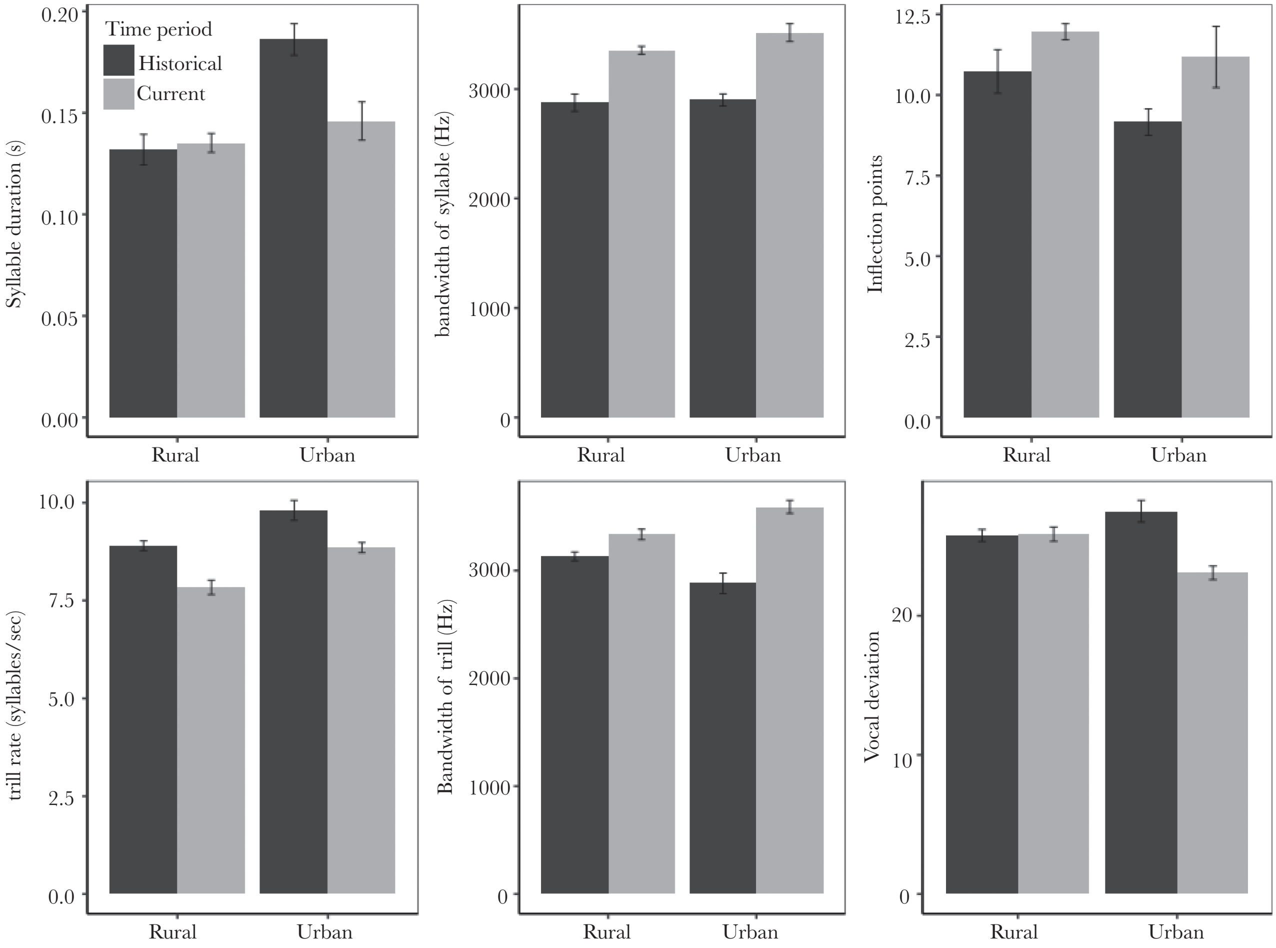

Figure 2

Plots of historical (black) and current (gray) song variables in rural and urban populations of white-crowned sparrows. The complex syllable duration of historical urban birds' songs was significantly longer than contemporary urban songs or any rural male songs. The bandwidth and number of inflection points of the complex syllable increased from historical to current songs in both urban and rural males. Historically, the trill rate was significantly greater and the bandwidth smaller in songs of both urban and rural males. Vocal deviation of the trill did not differ between historical and current rural songs but did significantly decrease from historical to current urban songs, resulting in contemporary urban birds having the highest vocal performance. Bars represent mean and standard error.

over time (Luther and Baptista 2010; Luther and Derryberry 2012; Moseley et al. 2018). We examined historical recordings of WCSP songs from the 1970s to address how animal behaviors change over time and if different environments are associated with differences in the adaptations and trajectories of animal behaviors. We found that the portions of songs used for mate attraction and territory defense have changed over nearly 50 years. Complex syllables increased in bandwidth and complexity over time. For all males, the trilled portion of the song slowed in terms of note rate but increased in bandwidth over time. Song performance, as measured by vocal deviation for the trills, improved over time in urban male songs but did not change in rural male songs. Thus, over a span of nearly 50 years, we find increases in song complexity for males from both urban and rural populations and increases in vocal performance only in urban males.

Taken together, rural populations' song parameters of complex syllable duration and vocal deviation were in line with the null hypothesis of no directional change over time, while all measured urban song parameters significantly changed over time. Chief among those changes was how the contemporary urban males sang a complex syllable with more inflection points (greater complexity) and in a shorter duration than their historical counterparts, which is consistent with our prediction of increased complexity in the presence of anthropogenic noise. In addition, we found increases in vocal performance of the simple trill for contemporary urban males; thus, we did not find support for our hypothesis of a trade-off between measures of performance, instead both measures of performance increased. One possible explanation for these results is increased pressure from sexual selection driving cultural evolution in urban populations.

More complex songs and notes, those with increased frequency modulations, carry more information about the quality of the signaler than simpler songs and notes (Catchpole and Slater 2003; Bradbury and Vehrencamp 2011). In fact, complexity, measured here as the number of frequency inflections, could be a different axis through which males reveal quality and their performance ability. Just as the complexity of songs is important for mimics (Catchpole and Slater 2003) and species with complex songs, such as wrens and European warblers (Catchpole 1980; Kroodsma 1980), syllable complexity could be an important component of performance in species with relatively simpler songs. We found that the complex syllables of contemporary songs have greater bandwidth, more inflections, and increased complexity than did historical songs. Added complexity in the form of additional inflection points would allow for more information about a signaler to be contained in their signals, which should elevate the probability of a response from potential rivals and mates. These complex syllables are used for individual recognition in another subspecies of WCSP, *Z. l. pugetensis* (Nelson and Poesel 2007), and our results raise an empirical question of how complex syllables function in male-male competition and mate choice and if signal complexity is a salient trait in terms of sexual selection.

A trade-off of more complex note structure but reduced vocal performance of coastal SWSP resulted in more salient signals to territorial rivals and local females (Ballentine 2006; Ballentine et al. 2013). We expected a similar trade-off in the urban male WCSP, where we expected bandwidth to be compromised which would have resulted in a lower vocal performance. Instead we found that vocal performance and complexity both increased in the urban male songs over time. Although we do not know the exact mechanism as to why vocal performance and complexity increased, as both cultural and genetic evolutionary mechanisms are plausible, but we posit the following hypotheses, which warrant future research. The potential mechanisms could be 1) increased sexual selection through male–male competition in the urban populations, which could result in increased vocal performance to outcompete rivals, 2) drift, or 3) an increased ability for behavioral plasticity through Immediate Signaling Flexibility (see discussion below).

The literature on vocal performance indicates the importance of bandwidth and trill rate for sexual selection, as it is physiologically difficult to produce notes with greater bandwidth at fast repetition (reviewed by Podos et al. 2009). In maximizing their ability to perform this trade-off, males may reveal their quality to receivers (Byers et al. 2010). One inference of these studies is that by raising the minimum frequency, the singer limits the potential frequency bandwidth achieved in their song. Although we did find increases in minimum frequency in the urban songs sampled in this study and in previous studies of WCSP (Luther and Baptista 2010; Luther and Derryberry 2012; Derryberry et al. 2016), counter to our prediction, contemporary urban males sang at wider frequency bandwidths than historical urban males, which would indicate a relative increase in maximum frequency of current songs, as found by Luther and Derryberry (2012) and Luther et al. (2015). Increases in frequency bandwidth concomitant with raising the minimum frequency, most likely as a result of natural selection from anthropogenic noise, suggest increased pressure from male–male competition for a wide range of frequency bandwidth in contemporary urban habitats, which could be a result of increased competition over available territories or increased density in quality territories.

Background noise negatively influences vocal performance at the level of the individual, in that male WCSP on territories with greater low-frequency ambient noise have lower vocal performance (Luther et al. 2015). On the surface, our result of contemporary urban males singing songs with higher vocal performance than they did historically appears to contradict the findings of Luther et al. (2015); however, our present study does not assess territory level noise for individual urban males; instead, we are assessing population-level variation. There is a large amount of spatial variation in the amplitude of anthropogenic noise in the city (San Francisco Department of Public Health 2008; Derryberry et al. 2016), which could help to explain why we found that current males have greater vocal performance compared with historical urban or rural males, despite more contemporary anthropogenic noise. Alternatively, it is possible that despite the increase in ambient noise over time, urban males have found ways to increase their vocal performance and increase their opportunities for mate attraction. For example, a recent playback experiment shows that bandwidth, but not trill rate, is salient for male–male competition in urban WCSP, suggesting that the patterns we find here of broader bandwidth over time have functional consequences (Phillips and Derryberry 2018). Furthermore, increases in territory noise correlate with increases in aggression to all levels of vocal performance, which could influence the strength of male competition acting on songs (Phillips and Derryberry 2018).

Generally, birds in urban environments tend to exhibit more behavioral flexibility than those that do not inhabit urban environments (McKinney 2006; Bonier et al. 2007; but see Marzluff 2017). The increase in behavioral flexibility could be a result of phenotypic plasticity that is greater for urban than rural populations or possibly selection for certain personalities, such as bold, aggressive, neophilic, and social, in cities (Lowry et al. 2013; Møller et al. 2015). The increased behavioral flexibility and/or bolder personalities could allow urban birds to increase the vocal parameters of their songs in ways that rural birds do not, which might lead to the different trajectories of vocal performance observed in this study.

One specific aspect of behavioral flexibility is immediate singing flexibility (ISF), which is a mechanism by which animals can adjust their signals in immediate response to their environment to improve signal salience. However, ISF is not thought to have longer-term effects beyond the immediate response, as it is instantaneous, and therefore an unlikely explanation for the measurements of the entire sample of contemporary urban songs. Many birds are capable of ISF in the presence of relatively loud background noise and adjust their signals to reduce the contrast with the background noise or increase the signal redundancy to improve signal salience (Slabbekoorn 2013). In fact, urban but not rural WCSP have been shown to exhibit ISF (Derryberry et al. 2017; Gentry and Luther 2019). However, it has also been noted that the ISF adjustments of WCSP do not affect the trill portion of the song or their vocal performance (Gentry et al. 2017); thus, we do not suspect that ISF or behavioral flexibility explains the changes in songs that are observed in the current study. For WCSP that crystalize only one song type, ISF would more likely be observed in spectral features such as frequency in the presence of noise, whereas the notes of a complex syllable are learned and reproduced in a stereotyped fashion.

Song learning is influenced by components of the local environment, such as habitat structure, social structure, and background noise. For example, relatively loud low-frequency noise can affect the acquisition and vocal production of songs in the next generation (Peters et al. 2012; Moseley et al. 2018). Ultimately, vocalizations with the greatest bandwidth or note rate are most likely to get the strongest responses from rival males (Moseley et al. 2013; Phillips and Derryberry 2017), which indicates vocal performance is a salient signal in competition for territories. Observed increases in vocal performance over time suggest a potential heightening of sexual selection pressures in the city when compared with rural populations. Increase in population density, and subsequent intraspecific competition, of birds in cities (Kokko and Rankin 2006; Shochat et al. 2006) is one potential explanation for an increase in sexual selection pressure of birds in cities. However, further work is needed to examine whether other species in urban habitats are exhibiting increased sexual selection pressures or changes in sexually selected traits over time.

At our study locations, both urban and rural habitats have changed over a nearly 50-year time period with the urban region increasing in anthropogenic noise in the low-frequency bands (Luther and Derryberry 2012) and the vegetation changing from mostly grassland to more dense scrub vegetation in the rural habitats (Derryberry 2009). These physical and acoustic changes have most likely influenced how the songs of WCSP have changed over time. In the city, WCSP have increased the minimum frequency of their songs in the past 50 years (Luther and Baptista 2010; Luther and Derryberry 2012), as has been found in other species exposed to anthropogenic noise around the world (Shannon et al. 2016), whereas rural WCSP songs have previously been shown to reduce their trill rate and increase their bandwidth over a 35-year period in response to denser vegetative structure (Derryberry 2009). The present study supports both of these findings and also identifies increased vocal complexity and vocal performance in contemporary compared with historical songs.

Results from this study suggest that although contemporary urban male WCSPs may risk diminished signal salience from higher song minimum frequencies and slower trill rates, they may compensate for this loss by increasing overall vocal performance. We suggest that cultural evolution has enabled this rapid shift in song complexity and vocal performance, which might otherwise not be possible for species that do not learn their vocalizations. Another line of inquiry could investigate species that do not learn their vocalizations to determine whether changes in their vocalizations have proceeded along similar trajectories. Our results open the door to many new questions regarding the relationships of urban habitats, anthropogenic noise, vocal performance, and sexual selection that will lead to a heightened understanding of how animals respond and persist in modified habitats with broad applications in the fields of behavioral ecology, ecology, evolution, and conservation biology.

FUNDING

This work was supported by the National Science Foundation Integrative Organismal Systems (grant numbers 1354763 and 13547756) to E.P.D. and D.A.L.

This project would not have been possible without data collected by Dr. Luis Baptista and Dr. Baker. We thank Dr. Kate Gentry for advice on song measurements and statistical analyses, and Evan Lamb for data processing of the complex syllable. Tulane Institutional Animal Care and Use Committee (IACUC) and National Park Service IACUC approved this research (protocol 0427-R). Permission for research in the urban sites was granted by the Golden Gate National Recreation Area (SCI-0007), the San Francisco Parks and Recreation (041415), and the Presidio Trust and in the rural sites by the Point Reyes National Seashore (SCI-0016).

Data Accessibility: Analyses reported in this article can be reproduced using the data provided by Moseley et al. (2019).

Handling editor: Ulrika Candolin

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