

# The learning advantage: bird species that learn their song show a tighter adjustment of song to noisy environments than those that do not learn

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 song learning;  
 song plasticity;  
 suboscine;  
 urban noise.

## Abstract

Song learning has evolved within several avian groups. Although its evolutionary advantage is not clear, it has been proposed that song learning may be advantageous in allowing birds to adapt their songs to the local acoustic environment. To test this hypothesis, we analysed patterns of song adjustment to noisy environments and explored their possible link to song learning. Bird vocalizations can be masked by low-frequency noise, and birds respond to this by singing higher-pitched songs. Most reports of this strategy involve oscines, a group of birds with learning-based song variability, and it is doubtful whether species that lack song learning (e.g. suboscines) can adjust their songs to noisy environments. We address this question by comparing the degree of song adjustment to noise in a large sample of oscines (17 populations, 14 species) and suboscines (11 populations, 7 species), recorded in Brazil (Manaus, Brasilia and Curitiba) and Mexico City. We found a significantly stronger association between minimum song frequency and noise levels (effect size) in oscines than in suboscines, suggesting a tighter match in oscines between song transmission capacity and ambient acoustics. Suboscines may be more vulnerable to acoustic pollution than oscines and thus less capable of colonizing cities or acoustically novel habitats. Additionally, we found that species whose song frequency was more divergent between populations showed tighter noise–song frequency associations. Our results suggest that song learning and/or song plasticity allows adaptation to new habitats and that this selective advantage may be linked to the evolution of song learning and plasticity.

## Introduction

Although most birds vocalize, vocal learning has evolved only within a restricted number of taxa (Kroodsma, 1982, 2004). It has been found so far in only three bird orders: Apodiformes (hummingbirds), Psittaciformes (parrots) and Passeriformes (perching birds). Notably, two large taxonomic groups within the

passerines differ in whether songs are learnt (oscines) or not (suboscines). Numerous hypotheses have been proposed to explain the evolution of vocal learning, ranging from adaptive explanations to side effects of correlated processes (review in Podos & Warren, 2007). In 1979, Hansen proposed that song learning would allow birds living in a particular habitat to select those songs with the acoustic characteristics that best transmit in that environment (Hansen, 1979). A number of studies within and between bird species have documented that song design matches those patterns that transmit well in the specific ambient in which they are produced (e.g. Krebs & Davies, 1993; Buskirk, 1997; McCracken & Sheldon, 1997; Slabbekoorn, 2004; Seddon, 2005). Hansen's hypothesis implies that song learning would allow a faster adaptive song modifica-

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tion than natural selection on genetic differences in song (Hansen, 1979). Yet, no formal test of this hypothesis has been conducted.

Oscine species differ from their sister group, the suboscines, in a number of ecological and natural history traits, aside from their differences in song ontogeny. Oscines have undergone extensive geographical radiation, whereas suboscines occur mostly in tropical regions of the Americas (ca. 1000 species) with only a few species in Africa and Asia (Ericson *et al.*, 2003; Barker *et al.*, 2004; Moyle *et al.*, 2006). In terms of colonizing different types of habitats, oscines are among the most successful groups of birds, whereas suboscines are predominantly found in the tropics and subtropics, suggesting particular adaptations to certain ecological conditions which may restrict their abilities to colonize and expand their ranges (Feduccia, 1999; Stutchbury & Morton, 2001). For instance, the metabolic capacity of oscines has been found to be higher than that of suboscines, and this could limit range expansions and restrict radiations (Swanson & Bozinovic, 2011).

One possible test of the selective advantage of song learning is to analyse whether song learners are in some way better at communicating in novel environments than non-song learners. Because in most suboscines studied so far (review in Kroodsma, 1982, 2004), vocal imitation does not occur, it can be hypothesized that they possess a lower capacity to adapt their song to new environments than oscine birds. Mechanisms of song adaptation to the habitat are important because bird song is involved in mate choice and territorial defence, both of which have a great impact on reproduction (Catchpole & Slater, 2008). A context in which this may be currently relevant is urban colonization.

In recent years, several studies have shown that songbirds modify their song in response to noise in urban areas, similar to what they do in natural noisy environments (reviews in Brumm & Slabbekoorn, 2005; Patricelli & Blickley, 2006; Ríos-Chelén, 2009). These modifications include an increase in vocalization loudness as noise increases, a phenomenon known as the Lombard effect (Brumm, 2004); singing with increased redundancy (Brumm & Slater, 2006); or singing at a higher pitch (Slabbekoorn & Peet, 2003; Fernández-Juricic *et al.*, 2005; Slabbekoorn & den Boer-Visser, 2006; Wood *et al.*, 2006; Bermúdez-Cuamatzin *et al.*, 2009; Hu & Cardoso, 2009; Nemeth & Brumm, 2009; Francis *et al.*, 2011a). In particular, increases in minimum song frequency in response to noise have been reported in a wide range of oscine species. These shifts are hypothesized to increase the chances of being heard in noisy urban environments, particularly because urban noise is characterized by low frequencies, and frequency shifts that reduce the overlap with noise would be selected for, although a recent study concludes that the advantage gained by this strategy

would be lower than using an increase in amplitude (Nemeth & Brumm, 2010). Similarly, shifts towards lower song frequencies have been found in a bird species living in forest in which the main source of noise is high-pitched insect calls (Kirschel *et al.*, 2009). However, some authors have indicated that noise is not the only difference between urban and natural habitats and that other factors may introduce relevant selection pressures (Warren *et al.*, 2006; Mockford *et al.*, 2011).

Recently, Francis *et al.* (2011b) found that among the two suboscine species they studied, the ash-throated flycatcher (*Myiarchus cinerascens*) changed its song frequency with noise, whereas the grey flycatcher (*Empidonax wrightii*) did not. These contrasting patterns could be taken to suggest that species lacking song learning may be limited in their capacity to adapt to new and noisy environments (Rabin & Greene, 2002). However, a larger data set is necessary to properly evaluate this hypothesis.

Changes in song attributes to avoid noise masking can be due to short- or long-term processes (Brumm & Slabbekoorn, 2005; Patricelli & Blickley, 2006). In the short term, individuals may modulate vocal attributes as a response to current noise levels, including real-time frequency shifts (Tumer & Brainard, 2007; Gross *et al.*, 2010; Verzijden *et al.*, 2010; Bermúdez-Cuamatzin *et al.*, 2011), increased signal tonality (Hanna *et al.*, 2011) or choice of songs with particular song frequency elements within a repertoire (Halfwerk & Slabbekoorn, 2009). Long-term changes can involve (1) natural selection of better-adapted song genotypes, (2) cultural selection in which individuals learn those songs or song attributes that are more easily detected in noisy conditions (Slabbekoorn & Peet, 2003; Luther & Baptista, 2010) or (3) dispersal processes by which birds would establish territories in those habitats in which their song is more audible (a possibility that remains unexplored). Short-term adjustments require either a good degree of song plasticity or the capacity to pick and choose elements from a large song repertoire, whereas cultural selection will only be expected from birds that learn their songs (Rabin & Greene, 2002). Thus, it is to be expected that birds singing simple and stereotyped songs and lacking song learning, such as the suboscines, would show a weaker adaptation to new acoustic conditions than oscines, as cultural evolution is expected to allow faster character divergence than natural selection (Cavalli-Sforza & Feldman, 1981).

In this study, we explored in a large number of oscine and suboscine species the extent of the association between noise level and song frequency. We predicted that oscine songs would show higher levels of adjustment to urban noise than suboscine songs. As songs of species with lower frequencies are expected to be particularly masked by urban noise (Hu & Cardoso, 2009), we tested whether species-specific minimum song frequency could explain the variance in the

**Table 1** Bird species recorded in different cities. Number of individuals recorded is indicated below each city.

Group	Species	Brasilia	Curitiba	Manaus	Mexico DF
Oscines	<i>Ammodramus aurifrons</i>			17	
	<i>Cyclarhis gujanensis</i>	13			
	<i>Saltator similis</i>			31	
	<i>Sicalis flaveola</i>		17		
	<i>Sporophila nigricollis</i>	23			
	<i>Thraupis episcopus</i>			31	
	<i>Thraupis sayaca</i>		30		
	<i>Troglodytes musculus</i>	14	31	24	
	<i>Turdus ignobilis</i>			20	
	<i>Turdus leucomelas</i>			23	
	<i>Turdus rufiventris</i>		34		
	<i>Vireo olivaceus</i>			20	
	<i>Volatinia jacarina</i>	38			
<i>Zonotrichia capensis</i>	17	29			
Suboscines	<i>Cranioleuca obsoleta</i>		30		
	<i>Elaenia parvirostris</i>		21		
	<i>Furnarius rufus</i>	17	26		
	<i>Pitangus sulphuratus</i>	19	40	15	
	<i>Pyrocephalus rubinus</i>				28
	<i>Tyrannus melancholicus</i>		27	17	
	<i>Tyrannus savana</i>	22			

strength of the association between song change and noise. Additionally, because the evolution of complex and variable songs has been associated with the occurrence of song learning (Kroodsmma, 1982) and song learning has been linked to the origin of geographical variation of songs (Mundiger, 1982), we assessed whether the degree of song differentiation between populations was a predictor of the level of song adaptation to noise in urban conditions, expecting species with highly divergent songs to show stronger associations between minimum song frequency and noise levels.

## Materials and methods

### Study sites and subjects

We recorded songs of 28 avian populations, belonging to 21 different species in a variety of public gardens, parks and avenues in cities of Mexico (Mexico City) and Brazil (Manaus, Brasilia and Curitiba). Of these, 17 populations belong to oscine species (14 species) and 11 populations to suboscine species (seven species, see Table 1 for a list of species and sample sizes). Sample size varied from 13 to 40 individuals per population. We use a conservative definition of population, encompassing all individuals of the same species inhabiting the ensemble of locations (parks and gardens) within the same city, as we assume that although some degree of geographical isolation may exist between the different parks of the same city (Björklund *et al.*, 2010), the likelihood of gene exchange is far greater than between the different cities that we have chosen to study.

### Song recordings and noise measures

We recorded songs with a Sennheiser<sup>TM</sup> shotgun microphone (K6 + ME66) (Sennheiser Electronic Corporation, Wedemark, Germany) connected to a Marantz<sup>TM</sup> PMD660 digital recorder (D&M Holdings Inc., Kawasaki, Japan), or with a Telinga<sup>TM</sup> Pro7 parabolic microphone (Telinga Microphones of Sweden, Uppsala, Sweden) connected to an Edirol<sup>TM</sup> R-09 digital recorder (Roland Corporation, Hamamatsu, Japan). Recordings (24 kHz sampling rate, 16 bit accuracy) were mostly taken during the morning (1 h before to 2 h after sunrise). Birds were recorded from a distance of 5–10 m, and this distance did not seem to vary systematically between bird species. When a source of noise (e.g. a highway) was evident, we took care to place ourselves between the source of the noise and the subject, so that the recording would be less noisy. Immediately after a bird was located and successfully recorded (1–5 min), noise levels were measured for 1 min with a sound level meter SEW<sup>TM</sup> 3210 SL (Standard Electric Works, Co., Ltd, New Taipei City, Taiwan; ANSI S1.4 type II) (A-weight and slow response settings; range 32–130 dB) at 10-s intervals with the equipment pointing upwards, held vertically at an arm's length from the observer.

### Song measurements

Spectrograms were calculated with Raven<sup>TM</sup> software (Cornell Laboratory of Ornithology, Ithaca, NY, USA) version 1.3 (window Hann, DFT size: 512 samples, overlap 50, filter bandwidth 124 Hz, in which one cursor movement amounted to a difference of 16.7 Hz in

the frequency axis and to 0.002 s in the time axis). These parameters were decided upon visual inspection of examples of several species using a variety of frequency spectrum settings. The following measures were taken: song length (s), song minimum and maximum frequency (the lowest and highest frequencies in the song, respectively, in Hz), peak frequency (frequency with the highest amplitude in the song), number of total syllables (elements with a continuous trace in the spectrogram) in a song and size of within-song syllable repertoire (i.e. number of different syllable types in a song). We divided the number of different syllable types in a song between the total number of syllables to obtain a measure of song versatility.

We avoided measuring those songs whose minimum frequencies were not discernible from the background noise (this situation was found in a very limited number of occasions as we always recorded facing away from noise sources). Thus, a bias on our results due to background noise masking the minimum frequency of songs is unlikely. Furthermore, because our tests involve comparing different species inhabiting the same location, this possible source of error is expected to affect all species similarly and thus would not contribute to differences between species.

### Geographical song variation

To generate estimates of within-species geographical song variation, we obtained additional recordings for all studied species from the Macaulay Sound Library (<http://macaulaylibrary.org>), the Xeno-canto sound collection ([www.xeno-canto.org](http://www.xeno-canto.org)) and the sound library of the Museo Nacional de Ciencias Naturales (Madrid) to complement our own field recordings. For each species, we chose good-quality recordings from one individual from each of several populations across South America, spanning as much as possible the whole geographical range of each species, from Venezuela to Argentina (average distance between populations per species 2005.7 km, SD = 624.4). We obtained and analysed an average of 5.29 (SD = 3.6) consecutive songs per individual from an average of 12.28 (SD = 2.7) populations (Appendix 1). We used one individual to represent each population because our data showed that variation between populations was far larger than within populations for all variables measured (all ANOVAS,  $P < 0.001$ ). Measurements were identical to those used in the analysis of our own recordings. A principal component analysis was used to derive three independent components that measured song frequency (PC1; 37.6% of variance explained), syllable repertoire size and song length (PC2; 30.5%), and song versatility (PC3; 20.39%; see Table 2 for details). Values of the different songs from each individual were averaged for each component. Data were then classified by species, and pairwise standard deviations were calculated for each

**Table 2** Loadings of the different song measurements on the principal components extracted. Figures in bold represent those loadings that have been selected to represent the meaning of each component.

Song measurement	PC1	PC2	PC3
Song length	-0.113	<b>0.893</b>	0.139
Minimum frequency	<b>0.859</b>	-0.318	0.063
Maximum frequency	<b>0.870</b>	0.126	0.265
Peak frequency	<b>0.944</b>	-0.094	0.190
Syllable repertoire size	-0.096	<b>0.565</b>	0.756
Number of syllables	0.310	<b>0.866</b>	-0.274
Song versatility	-0.361	-0.384	<b>0.807</b>
Explained variance	37.6%	30.5%	20.39%

component between each pair of possible population combinations. Thus, for each species, three song-distance half-matrixes were built, one per principal component. Each of these three half-matrixes was regressed on a geographical distance half-matrix that measured (km) the distance between each population pair. Using these linear equations, we obtained for each principal component the expected song-deviation at 1000 km. This arbitrary distance was chosen because it lies roughly in the middle of the obtained length of the geographical distributions for most species. Thus, our measure represents the average standard deviation between populations for each song component.

### Statistical analyses

All song variables were log-transformed to obtain normally distributed data. For each species, we ran GLMM models in SAS<sup>TM</sup> (Proc Mixed; Cary, NC, USA) relating frequency measures to noise amplitude (dBA). We corrected for the possible bias of number of localities by declaring the locality code as a random variable. Degrees of freedom were calculated using the Satterthwaite approach. Effect size ( $r$ ) was calculated from the  $F$  value of the fixed factor (noise), adjusted to the degrees of freedom of the model (Rosenthal, 1991).

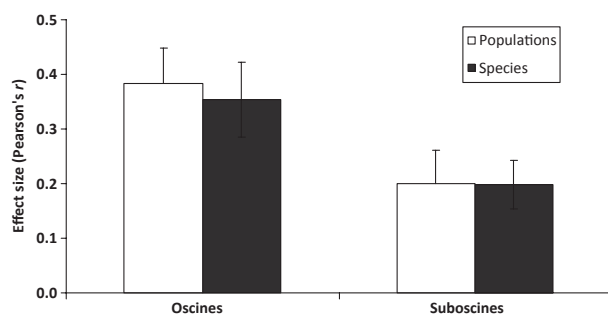
The contrast between oscines and suboscines cannot, by definition, be controlled phylogenetically. However, analyses relating effect sizes to differences between populations or species in song characteristics or geographical song variation estimates were performed also by computing independent contrasts using the software CAIC (Purvis & Rambaut, 1995). The analysis of contrasts was performed by running linear regressions through the origin (Felsenstein, 1985). Required assumptions for independent contrasts were met in our analyses (Purvis & Rambaut, 1995).

### Results

The average correlation between minimum frequency and noise level (effect size) was positive and signifi-

**Table 3** Summary of effect sizes found across the sample of different populations. Statistics ( $F$  and d.f.) represent the results of general mixed lineal models in which the effect of noise levels is added as a covariate (estimate). Effect sizes (Pearson's  $r$ ) are calculated from these statistics. S, suboscine, O, oscine.

Species	Locality	Suboscine	$F$	d.f.	$n$	Estimate (SE)	Effect size
<i>Ammodramus aurifrons</i>	Manaus	O	3.46	15	17	0.42 (0.22)	0.43
<i>Craniolaeca obsoleta</i>	Curitiba	S	0.29	6.61	30	0.21 (0.38)	0.21
<i>Cyclarhis gujanensis</i>	Brasilia	O	11.15	11	13	0.44 (0.12)	0.71
<i>Elaenia parvirostris</i>	Curitiba	S	2.3	19	21	0.46 (0.3)	0.33
<i>Furnarius rufus</i>	Brasilia	S	0.11	10.3	17	0.17 (0.49)	0.10
<i>Furnarius rufus</i>	Curitiba	S	1.28	18.9	26	0.71 (0.61)	0.25
<i>Pitangus sulphuratus</i>	Brasilia	S	0.38	17	19	-0.13 (0.19)	-0.15
<i>Pitangus sulphuratus</i>	Curitiba	S	0.43	38	40	0.17 (0.25)	0.11
<i>Pitangus sulphuratus</i>	Manaus	S	8.19	13	15	0.89 (0.31)	0.62
<i>Pyrocephalus rubinus</i>	México DF	S	0.05	26	28	-0.03 (0.1)	-0.04
<i>Saltator similis</i>	Manaus	O	1.66	29	31	0.29 (0.22)	0.23
<i>Sicalis flaveola</i>	Curitiba	O	0.5	14	17	-0.15 (0.21)	-0.19
<i>Sporophila nigricollis</i>	Brasilia	O	1.99	13.9	23	0.33 (0.22)	0.35
<i>Thraupis episcopus</i>	Manaus	O	7.08	22.8	31	1.08 (0.4)	0.49
<i>Thraupis sayaca</i>	Curitiba	O	0	21.7	30	-0.02 (0.29)	0.00
<i>Troglodytes musculus</i>	Brasilia	O	3.79	12	14	0.58 (0.29)	0.49
<i>Troglodytes musculus</i>	Curitiba	O	25.2	29	31	0.86 (0.17)	0.68
<i>Troglodytes musculus</i>	Manaus	O	11.26	22	24	0.87 (0.25)	0.58
<i>Turdus ignobilis</i>	Manaus	O	2.98	15.5	20	0.27 (0.15)	0.40
<i>Turdus leucomelas</i>	Manaus	O	7.27	20.9	23	0.43 (0.15)	0.51
<i>Turdus rufiventris</i>	Curitiba	O	0.52	14.5	34	0.14 (0.18)	0.19
<i>Tyrannus melancholicus</i>	Curitiba	S	1.3	25	27	0.16 (0.13)	0.22
<i>Tyrannus melancholicus</i>	Manaus	S	1.46	15	17	0.21 (0.17)	0.30
<i>Tyrannus savana</i>	Brasilia	S	1.51	20	22	0.22 (0.17)	0.26
<i>Vireo olivaceus</i>	Manaus	O	0.37	18	20	0.05 (0.07)	0.14
<i>Volatinia jacarina</i>	Brasilia	O	13.92	15.42	38	0.7 (0.18)	0.69
<i>Zonotrichia capensis</i>	Brasilia	O	9.01	10.7	17	0.46 (0.15)	0.68
<i>Zonotrichia capensis</i>	Curitiba	O	0.45	18.7	29	0.09 (0.12)	0.15



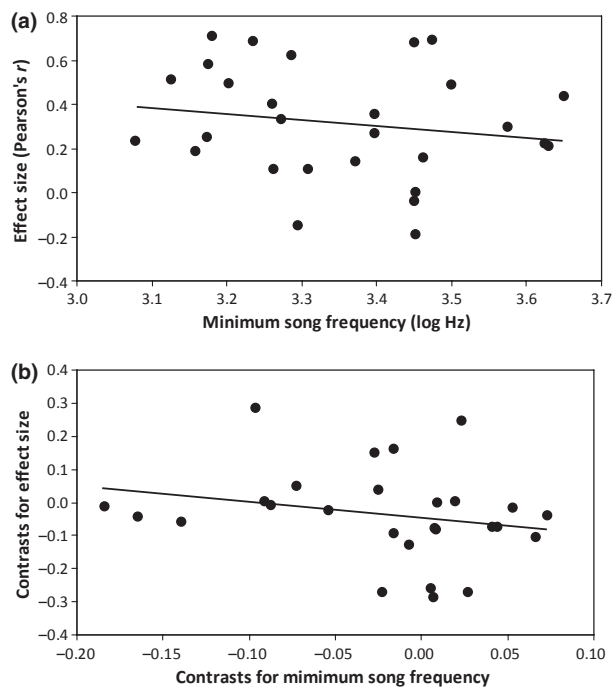
**Fig. 1** Comparison of effect size (Pearson's correlation coefficient obtained from correlating noise level with minimum song frequency) between populations and species of oscines and suboscines. Effect size was stronger in oscines than in suboscines, both when comparing between populations and between species.

cantly greater than zero, regardless of whether the sampling unit was populations or species [populations: mean  $r = 0.31$  (SE = 0.04),  $t_{27} = 6.50$ ,  $P < 0.001$ ; species: mean  $r = 0.30$  (SE = 0.05),  $t_{20} = 6.04$ ,  $P < 0.001$ ; see Table 3 for a list of population-specific effect sizes]. In a GLM controlling for sample size (number of birds

recorded per population), populations of oscine species showed larger effect sizes than suboscines ( $F_{1,26} = 5.09$ ,  $P = 0.033$ ,  $r^2 = 0.13$ ; Fig. 1). The same pattern emerged when the analysis was performed using species instead of populations as unit of analysis ( $F_{1,19} = 4.73$ ,  $P = 0.042$ ,  $r^2 = 0.15$ ; Fig. 1).

As low-pitched songs are more likely to be masked by urban noise, we expected effect sizes to be larger for species that sing low-pitched songs than for those that sing high-pitched songs. However, population-specific minimum song frequency was not related to effect size (minimum frequency:  $F_{1,24} = 1.19$ ,  $P = 0.23$ , Fig. 2a). A regression of independent contrasts through the origin also failed to demonstrate such association ( $F_{1,26} = 0.04$ ,  $P = 0.53$ ,  $B = -0.25 \pm 0.38$  SE, Fig. 2b).

If singing a large song repertoire allows birds to produce higher-pitched songs in response to noise, we would expect the degree of individual song variability to be positively related to effect size. However, effect size was not predicted by the degree of within-bout frequency variability ( $F_{1,24} = 2.04$ ,  $P = 0.16$ ). A regression of independent contrasts through the origin also showed the same lack of pattern ( $F_{1,26} = 2.29$ ,  $P = 0.14$ ,  $B = -1.05 \pm 0.69$  SE).

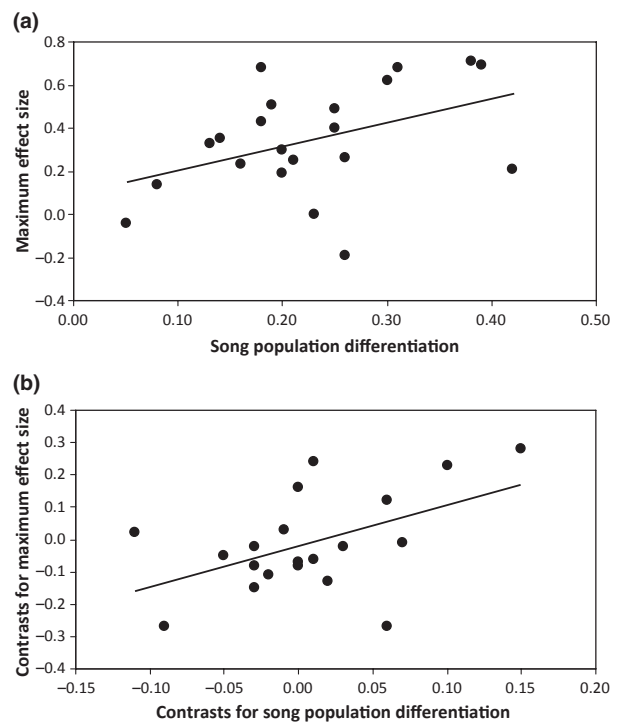


**Fig. 2** Population-specific minimum song frequency and lack of relationship with effect size (Pearson's correlation coefficient obtained as in Fig. 1) in regression with (a) log-transformed data and (b) independent contrasts through the origin. There is no association between minimum song frequency and effect size.

We calculated the degree of song differentiation between populations of the same species in an attempt to obtain a metric of song learning. We found that the degree of between-population song differentiation in song frequency was related to effect size: species with greater differences between populations in song frequency had larger maximum effect sizes ( $F_{1,19} = 6.71$ ,  $P < 0.05$ ;  $r^2 = 0.26$ ,  $B = 1.54 \pm 0.59$  SE; Fig. 3a). Independent contrasts through the origin confirmed this association ( $F_{1,19} = 5.99$ ,  $P < 0.05$ ;  $r^2 = 0.24$ ;  $B = 1.24 \pm 0.50$  SE; Fig. 3b). Neither between-population song differentiation in syllable repertoire size nor song versatility showed a significant relationship with effect size (data not shown). Despite our predictions, oscines and suboscines did not differ in any of these measures of song differentiation between populations (song frequency:  $t_{19} = -0.08$ ,  $P = 0.94$ , syllable repertoire size:  $t_{19} = -0.17$ ,  $P = 0.86$ ; song versatility:  $t_{19} = -0.28$ ,  $P = 0.78$ ), suggesting that both cultural and genetic processes are related to song differentiation.

## Discussion

The strength of the association between noise amplitude and minimum song frequency was higher in oscines than in suboscines. This is consistent with our



**Fig. 3** Song population differentiation in song frequency within species and effect size (Pearson's correlation coefficient). There was a positive association between song population differentiation and effect size (a); this association was confirmed with independent contrasts through the origin (b)

hypothesis that song learning or song plasticity allows birds to achieve a greater adaptation of their songs to the acoustic conditions of the environment in which they live (Hansen, 1979). Additionally, the strength of the association was larger in those species with higher song frequency differentiation between populations. Yet, as the level of this song differentiation was not different between song learners (oscines) and nonlearners (suboscines), these results suggest that song adaptation to ambient noise is not uniquely favoured by song-learning processes. Rather, population divergence in different species may result from varying degrees of selective learning (Luther & Baptista, 2010) and natural selection. It is also possible that immediate song plasticity may be linked to song differentiation, although currently there are no data on this respect. Less complex syrinx and brain structures in non-song-learning species (Müller, 1878; Gaunt, 1983; Gahr, 2000), which may be linked to their incapacity to learn their songs or otherwise limit their capacity to shift the pitch of their songs in real time, may also limit the capacity of suboscines to tune the pitch of their songs to local noise conditions. Suboscines differ from oscines in the way that the air is managed to produce modulations of frequency, as they depend exclusively on air sacs, instead

of the specialized syringeal muscles of oscines (Amador *et al.*, 2008).

Simulations and empirical studies show that cultural evolution allows faster changes than natural selection (Hansen, 1979; Cavalli-Sforza & Feldman, 1981). As urban noise can be considered a relatively novel selective force in urban habitats, the stronger effect size that we found in oscines than in suboscines may be the result of selective learning in oscines and of additional natural selection in either group. If birds learn their songs and if these songs are filtered by ambient noise, it is expected that the songs of learning birds will be better tuned to transmit well in areas with different noise levels. On the other hand, those birds whose songs are not developed through a learning process (suboscines) will not be able to adjust their songs to different noise regimes by copying preferentially those songs or song features that are more easily detected in noisy habitats. Thus, our results could be taken to suggest that learning species have better-adapted songs to novel acoustically polluted environments because cultural evolution requires less time than natural selection to produce locally adjusted songs. This type of cultural evolution process has been studied in the white-crowned sparrow, *Zonotrichia leucophrys*, a species that has undergone strong changes in song frequency in the last 40 years (Luther & Baptista, 2010). We propose that differential learning of different song types due to ambient noise filtering may be more common than previously expected, and future studies should be aimed at testing this hypothesis.

Short-term adaptations in the form of behavioural plasticity may also account for the stronger effect size in oscines found in this study. There are at least five experimental studies in oscines showing that individuals are capable of immediately modulating the pitch of their songs, or song syllables, as noise levels increase (Tumer & Brainard, 2007; Halfwerk & Slabbekoorn, 2009; Gross *et al.*, 2010; Verzijden *et al.*, 2010; Bermúdez-Cuamatzin *et al.*, 2011), although so far this kind of experimental evidence is lacking in suboscines. Nevertheless, some suboscines species do show a degree of individual song plasticity, for instance by means of different song forms as well as by small variations in temporal and frequency song attributes of the same song type (e.g. Smith, 1988; Smith & Smith, 1992; Ríos Chelén *et al.*, 2005). We suggest that whether birds can display such plasticity or not may also be function of their capacity to learn different song types or syllables. Our data set does not allow us to differentiate whether the oscine advantage is due to greater learning ability (ontogeny) or higher vocal abilities at immediate shifts (immediate plasticity). However, the difference in effect size that we found between populations and species does suggest a role of ontogenetic processes.

We did not find that species with large repertoires showed a larger effect size, suggesting that acoustic

adaptation to noise is not (or not generally) implemented by selecting high-pitched song elements from a given repertoire, but rather by shifting upwards the pitch of the song elements (Bermúdez-Cuamatzin *et al.*, 2009).

We found that differences in song frequency did not account for differences in effect size, in contrast to previous studies (Hu & Cardoso, 2009; Francis *et al.*, 2011b,c) in which species with low-pitched songs were either more likely to be affected by noise or less able to enter urban environments than species with high-pitched songs. We do not have a specific hypothesis to explain this difference with previous studies, yet the response of different bird species/faunas to ambient noise depends on the sources of song variance available to them, which may promote different mechanisms of song adaptation (e.g. shifts in preferred times for singing or in the length of songs) and these need not be identical in all cases.

Why song learning has evolved, how is it maintained through evolutionary time and why some species exhibit it, whereas others do not? Several theories have been proposed to explain its origin (Aoki, 1989; Nottebohm, 1991; Morton, 1996), but none seems to apply to all species or be widely accepted. There is some support for the hypothesis that vocal imitation originated as a response to strong sexual selection in polygynous species (Kroodsma, 2004), in which song repertoires may have evolved through female choice (Catchpole, 1982). Alternatively, song learning may favour birds that incorporate into their repertoires those song types that better match the acoustic transmission characteristics of different environments (Halfwerk & Slabbekoorn, 2009). Whatever the origin of song learning, several adaptive functions have been proposed to explain why it is maintained: habitat matching (Hansen, 1979), assortative mating (Nottebohm, 1991) and song matching (Nottebohm, 1972; Payne, 1982). Each of these hypotheses proposes that learners may benefit from singing specific song types that vary between areas. Additionally, a recent nonadaptive hypothesis (Lachlan & Slater, 1999) suggests that the interaction of genes and culture can be sufficient to maintain song learning without learning promoting fitness. According to this 'cultural-trap' hypothesis, once learning has evolved, cultural processes can act independently to maintain learning, regardless of whether there exist adaptive advantages to song learning (see also Luther & Baptista, 2010; Cardoso & Atwell, 2011).

We have provided evidence that learning species may be more efficient at singing higher-pitched songs in noisy environments than nonlearners. This may imply that nonlearning species (i.e. most suboscines) can in principle be more vulnerable to acoustic pollution. However, suboscines may possess different strategies to overcome noise masking and its negative consequences, such as shifting their singing routines

to quieter times of the day (Fuller *et al.*, 2007) and singing at higher rates (Díaz *et al.*, 2011). Whether urban communities filter out differentially suboscine and oscine species is thus an open question that needs to be addressed in future.

Current biodiversity conservation agendas are directed at identifying species with high extinction susceptibility (e.g. Cardillo *et al.*, 2006; Thomas, 2008). Anthropogenic noise is an increasing cause of concern for natural populations (Barber *et al.*, 2010), and thus, our data suggest that conservation strategies should take into account the greater susceptibility of suboscine species to this source of pollution. Given that the highest richness of suboscines is found in Neotropical regions, strategies directed at limiting the extent of noise pollution on protected sites through Latin America should be encouraged.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** List of recordings used in the analysis of geographic variation.

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