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Songbirds learn songs least degraded by environmental transmission

Susan Peters¹, Elizabeth P. Derryberry^{2,3,*} and Stephen Nowicki¹

¹Department of Biology, Duke University, 130 Science Drive, Durham, NC 27708, USA

²Department of Ecology and Evolutionary Biology, Tulane University, Boggs 400, New Orleans, LA 70118, USA

³Museum of Natural Science, Louisiana State University, 119 Foster Hall, Baton Rouge, LA 70803, USA

*Author for correspondence (ederrybe@tulane.edu).

Communication depends on accurate reception of signals by receivers, and selection acts on signals to transmit efficiently through the environment. Although learnt signals, such as birdsong, vary in their transmission properties through different habitats, few studies have addressed the role of cultural selection in driving acoustic adaptation. Here, we present a test of the hypothesis that song-learning birds choose to copy songs that are less degraded by transmission through the environment, using swamp sparrows (*Melospiza georgiana*) as our study species. We found that all subjects discriminated between undegraded and naturally degraded song models, and learnt only from undegraded song models, demonstrating a role for cultural selection in acoustic adaptation of learnt signals.

Keywords: acoustic adaptation; song-learning; communication; signals; cultural selection

1. INTRODUCTION

Communication signals—such as colourful bird plumage and rapid cricket songs—degrade during transmission through the environment [1]. Because signal function depends on accurate reception by receivers, selection acts against signals that transmit poorly through the environment. For example, lizard dewlaps, visual signals used in mate choice and male–male competition, vary in spectral characteristics among populations based on differences in the light-transmission properties of their respective habitat [2]. Although natural selection explains signal adaptation to different habitats in some taxa, little is known about the mechanisms underlying habitat-dependent selection on learnt signals, such as birdsong [3].

Because song transmission does not need to occur from parent to offspring [4] and can occur independently of fitness consequences associated with the song phenotype, natural selection alone cannot explain the widespread occurrence of acoustic adaptation of songs to habitats with different transmission properties [3]. In 1979 Hansen [5] hypothesized that ‘pupils’

may only copy the most clearly heard songs (i.e. those least degraded by the physical environment). If the pupil is the selective agent, then cultural selection rather than natural selection could drive habitat-dependent diversification of learnt signals. This hypothesis provides a plausible basis for understanding habitat-dependent song evolution, including response to recent selection pressures from urban noise [6].

We present a direct test of this hypothesis by hand-rearing male swamp sparrows (*Melospiza georgiana*) in the laboratory, and exposing them during their critical learning period to undegraded songs and songs mildly degraded by propagation through a natural swamp sparrow habitat. We predicted that if acoustic degradation interferes with song-learning, then young males would copy only from undegraded song models.

2. MATERIAL AND METHODS

(a) Study organism

Swamp sparrows need to hear conspecific song to develop their species typical song [7], which is composed of notes grouped into a syllable that is repeated at a constant rate in a trill (figure 1). Males typically produce three different song types [8]. Different song types are differentially subject to degradation, in the form of reverberation, frequency-dependent attenuation and amplitude fluctuations [9]. Thus, young swamp sparrows encounter songs degraded to varying degrees during their song-learning period.

(b) Subjects

We collected nine males as nestlings in Crawford County, PA and hand-raised them in a sound isolation room where they were tutored as a group with recorded songs [7]. The following spring, males were put into individual sound isolation chambers (see the electronic supplementary material ‘equipment.docx’ file for equipment used).

(c) Song tutoring

The 16 source song types used as tutoring models were from 10 wild-caught swamp sparrow males recorded in the laboratory in a semi-anechoic chamber. We divided the 16 song types into two groups, maximizing acoustic dissimilarity between groups to facilitate copy recognition, but balancing acoustic differences overall to avoid bias in how songs might transmit in the environment. Each group had six unique song types (table 1, A–L) and shared two types (table 1, M and N). The two variants (degraded and undegraded) of M and N were distinct from each other, not only in acoustic fine detail but also in trill rate (degraded variant of M 18.6% slower than undegraded variant; degraded variant of L 31.8% faster than undegraded variant; table 2).

To create degraded songs (figure 1; audio files provided in the electronic supplementary material), we broadcast eight source song types in a swamp sparrow habitat and re-recorded them at a distance of 25 m from the source, the range of the distance across two typical swamp sparrow territories [8]. We digitized the degraded song types and measured them for comparison with the undegraded models (table 2).

Bouts of all 16 song types (eight undegraded and eight degraded) were arranged randomly on a tutoring programme. Each song was presented in a 3 min bout with songs repeated once every 10 s with 1 min of silence between each song type bout. Birds heard one bout of each of the 16 model songs twice daily. Tutoring began around 20 days of age (19.6 ± 0.3 , $x \pm$ s.e.) at the onset of the critical learning period for swamp sparrows [10] and lasted 12 weeks.

(d) Adult song recording and analysis

After song development was complete, we recorded the males to determine their adult song type repertoire. We made sound spectrograms of one exemplar of each song type sung by each male and of each model. Two researchers (S.P. and B. Ballentine) visually compared each student song with models and judged which were copies, taking into account both syllable morphology and trill rate. To prevent observer bias, we compared student songs with spectrograms of the undegraded model songs and the undegraded renditions of the songs presented as degraded models. The two observers agreed 100 per cent in their assessments.

To quantify copy quality, we used pairwise spectrogram cross-correlation analysis [11] to quantify the similarity of two signals with respect to duration, absolute frequency, modulations of frequency and amplitude. A score of 1.0 indicates that two signals are

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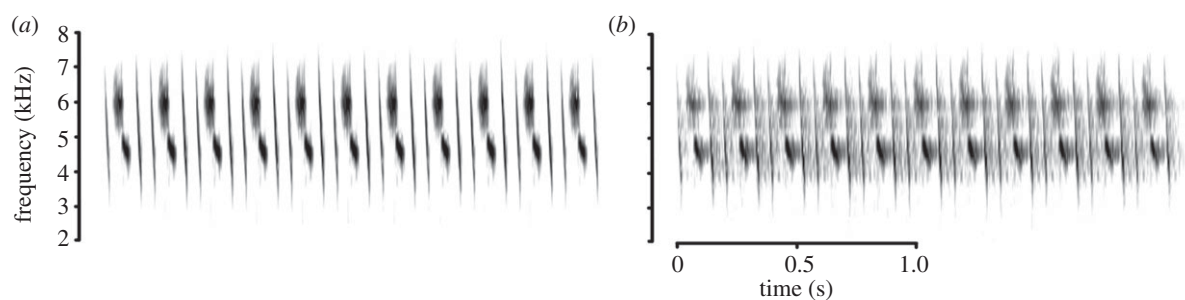


Figure 1. Typical swamp sparrow song composed of notes grouped into a syllable type repeated at a constant rate in a trill (type J, table 1, is shown). (a) Undegraded song: song recorded at 1 m from captive adult male. (b) Degraded song: song in (a) re-recorded at 25 m through natural habitat.

Table 1. Comparison of tutor song models and student copies of models.

tutor models				student copies			
model quality	syllable type	model	trill rate (Hz)	<i>n</i>	note cross correlation	syllable cross correlation	trill rate (Hz)
unique syllable types							
undegraded	A	sw17d	4.9	4	0.76 ± 0.02	0.55 ± 0.02	5.4 ± 0.1
undegraded	B	sw439c	7.0	1	0.83	0.72	7.3
undegraded	C	sw839b	6.0	2	0.80 ± 0.02	0.63 ± 0.06	6.6 ± 0.6
undegraded	D	sw18a	7.4	4	0.78 ± 0.05	0.64 ± 0.03	7.6 ± 0.2
undegraded	E	sw21b	11.5	1	0.83	0.68	12.9
undegraded	F	sw19b	7.7	1	0.68	0.50	7.1
degraded	G	sw849c	6.0				
degraded	H	sw439a	5.9				
degraded	I	sw439b	7.4				
degraded	J	sw13c	5.3				
degraded	K	sw23c	9.5				
degraded	L	sw22a	6.4				
shared syllable type							
undegraded	M	sw21a	7.0	2	0.79 ± 0.05	0.74 ± 0.10	7.1 ± 0.20
degraded	M	sw19c	5.7				
undegraded	N	sw22b	6.6	2	0.79 ± 0.03	0.53 ± 0.001	7.0 ± 0.43
degraded	N	sw17a	8.7				

identical. We digitized 10 renditions of each song type sung by each male and selected one syllable from the middle of each song. We divided each syllable into its component notes, and performed pairwise cross correlations between each of the 10 note renditions and the respective model note, as well as between each of the 10 renditions of the complete copy syllable and the complete model syllable.

We also compared student and model song trill rates, measuring the rate of five examples of each student song type and each model. Because copies may be sung slightly faster or slower than model rates, we report the rate comparisons between student rendition and model as the absolute value of the per cent difference [$100 \times (\text{student rate} - \text{model rate}) / \text{model rate}$].

(e) Signal synthesis and analysis

All songs were digitized at 25 kpts s^{-1} , analysis bandwidth of 0–10 kHz. Trill rates were measured from the waveform (time resolution = $\pm 2 \text{ ms}$). The maximum and minimum frequency for a song were measured from a spectrogram (256 point fast Fourier transform (FFT), frequency resolution = 98 Hz, time resolution: 10.2 ms) at -36 dB relative to the maximum level of the signal. Cross-correlation comparisons were performed between pairs of spectrograms (128 point FFT, frequency resolution = 195 Hz, time resolution = 5.1 ms).

3. RESULTS

The nine males sang a total of 20 song types, 17 of which were judged to be copies of tutor songs (representative tutor and student songs illustrated in figure 2; audio files provided in the electronic supplemental material). Males learnt solely from the undegraded

tutor models (binomial test: $p = 0.002$; table 1). The three pupil songs not assigned as copies had no similarity to any models. All syllables assigned as copies matched their respective models note for note. Copy accuracy (table 1) was comparable to previous studies of swamp sparrow copy quality and confirmed our visual assessments [12,13].

All of the undegraded models were learnt by at least one male. Thirteen of the 17 student syllables unambiguously matched a unique song type in the undegraded model group. Two males sang song type M, and two males sang song type N, both of which had a variant present in both the undegraded and degraded groups. The high cross-correlation scores for these copies indicate very good matches to the respective undegraded variant (table 1). Furthermore, the trill rates of these songs were much more similar to those of their respective undegraded variants than to the degraded variants ($5.1 \pm 2.9\%$ versus $27.3 \pm 3.2\%$ absolute trill rate difference to undegraded syllable types M and N versus degraded syllable types M and N, respectively). Thus, we are confident that males rejected all degraded song models, and that all undegraded songs were copied by at least one test subject.

Table 2. Analysis of variance of spectral and temporal features of undegraded song models, source for degraded song models and degraded song models.

song feature	undegraded model	source for degraded model	degraded model	<i>F</i> -ratio	<i>p</i> -value	d.f.
trill rate (Hz)	7.3 ± 0.7	6.9 ± 0.5	6.9 ± 0.5	0.15	0.86	2
maximum frequency (Hz)	7662 ± 207	7452 ± 134	7457 ± 123	0.57	0.58	2
minimum frequency (Hz)	2829 ± 110	2953 ± 137	2910 ± 175	0.19	0.83	2
bandwidth (Hz)	4833 ± 182	4499 ± 119	4547 ± 138	1.38	0.25	2
notes per syllable	3.4 ± 0.2	3.4 ± 0.2	3.0 ± 0.3	1.02	0.38	2
syllables per song	14.5 ± 1.4	13.9 ± 1.1	13.9 ± 1.1	0.09	0.91	2
song length (s)	2.0 ± 0.01	2.0 ± 0.02	2.0 ± 0.02	0.62	0.5	2

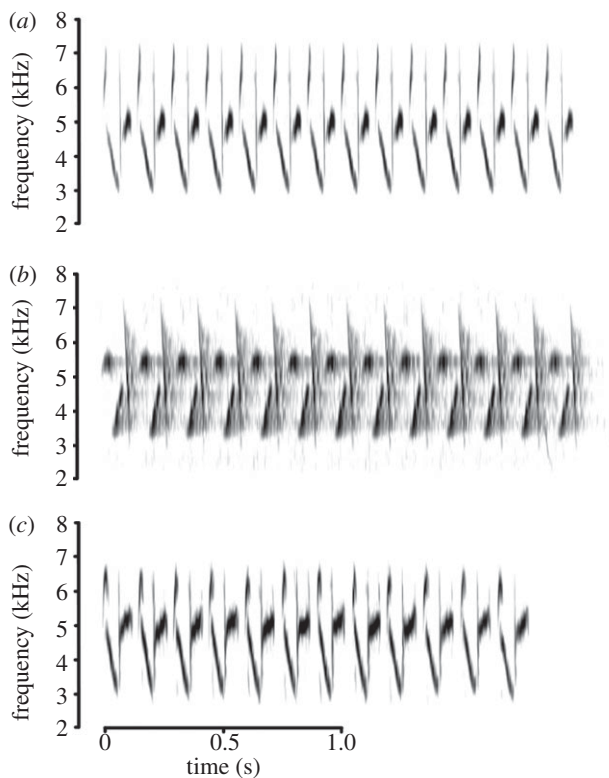


Figure 2. Sonograms of representative tutor and student songs. (a) Undegraded tutor model (type B, table 1), (b) degraded tutor model (type L, table 1), and (c) student copy of undegraded tutor model type B.

4. DISCUSSION

Our results clearly indicate that young male swamp sparrows differentially copy undegraded songs in the song-learning process. In fact, males rejected all degraded song models in our experiment. This result has broad implications for the role of cultural selection in acoustic adaptation of learnt signals. If birds preferentially learn less degraded songs, then songs would differentiate over time between habitats with different sound transmission properties. Cultural selection on song quality may therefore help explain the widespread pattern of habitat-dependent song diversification among bird species [3].

Our study is, to our knowledge, the first to provide strong support of the hypothesis that cultural selection can drive habitat-dependent diversification of learnt signals. An earlier study tested this hypothesis using Carolina wrens (*Thryothorus ludovicianus*) [14]. Four males were exposed to undegraded songs and songs degraded by playback in an echoic room. Although

males learnt more undegraded than degraded songs, only song models that were twice as degraded as naturally degraded song models were rejected. This study's interpretation was limited by its small sample size, by the artificial method of producing degraded song models, and by the fact that males did not reject song models with levels of degradation that they would encounter in a natural learning scenario. Our study found that all test subjects rejected naturally degraded song models, thus providing, to our knowledge, the first robust test of Hansen's hypothesis.

Our study does not address another mechanism proposed to explain acoustic adaptation of learnt signals, which is adult vocal plasticity. In some species, adults can adjust their singing behaviour (e.g. increase amplitude or preferentially sing particular song types) to transmit more effectively in their current environment [15]. Most studies on adult plasticity have been directed at behavioural responses to anthropogenic (e.g. urban noise) or natural ambient noise levels that can fluctuate dramatically over short time periods. However, individual vocal adjustment to environmental conditions alone cannot explain widespread habitat-dependent song differentiation across species. Cultural selection and vocal plasticity are not mutually exclusive. Cultural selection is a process that occurs over generations (e.g. from tutor to pupil), whereas adult vocal plasticity allows individuals to respond to immediate changes in the sound transmission environment. This study should inspire additional research on the developmental and behavioural mechanisms underlying habitat-dependent diversification of learnt signals.

All animal work was approved by the Duke University IACUC (protocol no. A240-96-5).

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