Behavioral Ecology and Sociobiology (2018) 72:47
https://doi.org/10.1007/s00265-018-2469-7

ORIGINAL ARTICLE

A test of the eavesdropping avoidance hypothesis as an explanation for the structure of low-amplitude aggressive signals in the song sparrow

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Received: 24 October 2017 / Revised: 2 February 2018 / Accepted: 13 February 2018

Abstract
Low-amplitude signals function in private exchanges of information between signalers and nearby receivers. The eavesdropping avoidance hypothesis proposes that selection favors quiet threat signals in order to avoid the costs of eavesdroppers. If true, then selection should favor other acoustic traits in addition to low amplitude that lead to quiet signals transmitting less effectively through the environment compared to broadcast signals. The "warbled" soft songs of male song sparrows differ from "crystallized" soft songs and from broadcast songs in a number of acoustic traits, suggesting that these songs may transmit less effectively. We tested this prediction in a field experiment by playing broadcast songs, crystallized soft songs, and warbled soft songs through a loudspeaker at the same amplitude and recording the propagated songs at five distances, at two heights, and in two different habitat types. Counter to our prediction, we found no evidence that either form of soft song transmits differently than broadcast song when all were played loudly. If anything, soft songs transmitted more effectively when all songs were played quietly. Our results do not support one prediction made by the eavesdropping avoidance hypothesis, although the possibility remains that reduced amplitude alone is sufficient to reduce eavesdropping. The question of why warbled soft song differs in acoustic structure remains unresolved.

Significance statement
Quiet aggressive signals are a puzzle because their meek form seems counter to their purpose—to threaten and intimidate rivals. One explanation for quiet signals is that reducing the signal's transmission range reduces the costs imposed by eavesdroppers, which predicts that quiet signals will transmit through the environment poorly relative to louder, broadcast signals. We tested this prediction by playing song sparrow "soft songs" and "broadcast songs" at the same amplitudes and measured their transmission properties at different distances and heights, and in two habitats. We found that soft and broadcast songs did not transmit differently when played loudly, and soft songs transmitted slightly better when played softly. Our results do not support the idea that quiet signals are explained by eavesdropping avoidance, at least not in the song sparrow.

Keywords Communication · Low amplitude · Eavesdropping avoidance · Signal degradation · Soft song · Song sparrow

Introduction

Recent years have seen rising interest in the role that amplitude plays in animal communication systems. Research has examined, for example, the various motivational and physiological reasons for modifying amplitude (Zollinger and Brumm 2015) and the response of signal receivers to amplitude variation (Ritschard et al. 2010, 2012). In particular, interest in low-amplitude signals has grown as these signals are increasingly documented across species and social contexts (Reichard and Anderson 2015). For instance, the lar gibbon

Communicated by B. Voelkl

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Published online: 26 February 2018

(*Hylobates lar*) produces a variety of low-amplitude close-range "hoo" calls across contexts such as male-female duetting, feeding, and alarm calling (Clarke et al. 2015). Male ring-tailed lemurs (*Lemur catta*) produce low-amplitude "purrs" during aggressive interactions (Bolt 2014). Croaking gourami (*Trichopsis vittata*) females produce low-amplitude "purring sounds" in the presence of courting males (Ladich 2007), and male golden rocket frogs (*Colostethus beebei*) produce rapid, low-amplitude courtship calls after a female approaches (Bourne et al. 2001). Thus, we see many instances in which signals appear to function in private exchanges of information between signalers and nearby receivers.

The low-amplitude signals of birds are intriguing because their apparently modest form seems antithetical to two of their dominant functions: to impress potential mates (Titus 1998; Reichard et al. 2011, 2013) and to threaten rivals (Akçay et al. 2015; Reichard and Welklin 2015). In particular, the quiet signals given during intraspecific competition are puzzling, especially since these signals are reliable threats of aggressive escalation in several species, including song sparrows (*Melospiza melodia*; Searcy et al. 2006), swamp sparrows (*Melospiza georgiana*; Ballentine et al. 2008), black-throated blue warblers (*Dendroica caerulescens*; Hof and Hazlett 2010), corncrakes (*Crex crex*; Rek et al. 2011), and brownish-flanked bush warblers (*Cettia fortipes*; Xia et al. 2013).

The notable connection between low-amplitude vocalizations and aggressive signaling in birds raises the question of why selection has repeatedly favored quiet signals in agonistic contexts. One widely cited explanation for low-amplitude signaling is the "eavesdropping avoidance hypothesis," which argues that signalers produce signals at reduced amplitudes to reduce transmission range and thereby avoid the costs associated with eavesdroppers (McGregor and Dabelsteen 1996). For example, individuals engaged in agonistic interactions may benefit from concealing their relative fighting abilities or the outcome of the contest from other potential competitors (McGregor 1993) or from mates or potential mates (McGregor and Dabelsteen 1996; Mennill et al. 2002). Predators are another class of eavesdroppers that may locate prey by listening to signals and may take advantage of prey that are distracted by signaling interactions (Ryan et al. 1982; Jakobsson et al. 1995; Mougeot and Bretagnolle 2000; Krams 2001).

If selection has favored low amplitude in aggressive signals to reduce eavesdropping, then other acoustic features that limit the range and detectability of these signals should have been favored as well (Akçay et al. 2015; Vargas-Castro et al. 2017). Balsby et al. (2003) tested this prediction by playing the loud "perch song" and relatively quiet "diving song" of whitethroats (*Sylvia communis*) at the same peak amplitude and found greater excess attenuation and lower signal-to-noise ratios for diving songs compared to perch songs that were transmitted across the same distances. In a similar study of the corncrake, Rek (2013) played soft and loud calls at the same amplitude and recorded the playbacks at increasing distance from a loudspeaker. At 40 m, the recorded soft calls showed more degradation (lower signal-to-noise ratios) than did the loud calls, in line with the eavesdropping avoidance hypothesis. Recently, Vargas-Castro et al. (2017) conducted a song transmission study of the broadcast syllables and soft syllables of white-throated thrushes (*Turdus assimilis*). When played at the same amplitude over increasing distance, soft syllables showed relatively greater excess attenuation, larger blur ratios, and lower signal-to-noise ratios, demonstrating greater degradation and reduced transmission range of soft syllables. Experimental manipulation of soft syllables to lower their frequency to the range of broadcast syllables resulted in similar transmission properties to those of broadcast syllables. Analysis of spectral traits of soft syllables showed that minimum frequency, peak frequency, bandwidth, and frequency overlap with background noise were the acoustic traits that most affected the reduced transmission range of soft syllables. These studies provide evidence for the eavesdropping avoidance hypothesis, suggesting that acoustic properties in addition to low amplitude can limit the active space of low-amplitude vocalizations.

Perhaps the best-studied case of low-amplitude song used in agonistic contexts is "soft song" in song sparrows. Song sparrow males sing repertoires with on average eight broadcast song types in our study population (Peters et al. 2000; Boogert et al. 2011). In addition to broadcast song, males sing two categories of soft song during aggressive interactions with other males. Crystallized soft songs are sometimes identical to broadcast song types with the only difference being amplitude, but can also be composed of a broadcast song type intermixed with notes and phrases found only in soft songs. In contrast, "warbled" soft songs are composed of a seemingly jumbled series of notes and phrases and are never sung at broadcast amplitudes (Anderson et al. 2008). Soft song was first described as an aggressive signal by Margaret Morse Nice in her classic study of song sparrow behavior (Nice 1943). Interest increased following the finding by Searcy and colleagues that soft song was the only signal in song sparrows that reliably predicted attack on a taxidermic mount (Searcy et al. 2006), a result that has been replicated in a western population of the species as well (Akçay et al. 2011). Only two studies have tested the function of soft song as it relates to the eavesdropping avoidance hypothesis. Contrary to the predictions of the hypothesis, soft song use decreased during simulated territorial intrusions that were coupled with a high risk of predation (via playback of alarm calls or predator vocalizations) (Searcy and Nowicki 2006; Akçay et al. 2016). In a second experiment by Searcy and Nowicki (2006), territory owners were removed and interactions were simulated on their territories using playback from two loudspeakers. The eavesdropping avoidance hypothesis predicts that territory owners would benefit from using soft song during agonistic interactions to avoid attracting the attention of third party males. Contrary to this prediction, intrusions by nearby males were more likely in trials in which the simulated owner replied to an intruder's songs using soft songs compared to trials in which the simulated owner sang broadcast songs. Although these functional tests failed to find evidence to support the eavesdropping avoidance hypothesis, they did not address another prediction of the hypothesis: that signals selected for low amplitude to minimize transmission will also show other acoustic design features that minimize transmission (Rek 2013; Vargas-Castro et al. 2017).

We tested the eavesdropping avoidance hypothesis by performing a signal propagation experiment similar to Rek (2013) and Vargas-Castro et al. (2017). Acoustic traits can reduce the transmission of sounds by increasing excess attenuation and degradation and by allowing greater masking by ambient noise (Searcy and Yasukawa 2017). Certain acoustic traits such as higher maximum frequency, broader bandwidth, and greater frequency modulation may lead to reduced signal transmission range and a smaller active space for acoustic signals (Dabelsteen 2005). In line with this idea, our previous work revealed a number of acoustic differences between soft song and broadcast song (Anderson et al. 2008): warbled soft songs are more variable than either crystallized soft songs or broadcast songs and contain fewer trills, greater variation in note composition, and unique note types not found in the broadcast song repertoire. Also, warbled soft songs have greater energy at both low frequencies (1–2 kHz) and high frequencies (9–10 kHz) compared to broadcast songs, with crystallized soft songs having intermediate values. We asked whether these acoustic differences make soft songs prone to a greater degree of excess attenuation and increased masking by noise, resulting in warbled soft songs degrading more over shorter distances as compared to broadcast songs. Because crystallized soft songs share acoustic traits with both broadcast songs and warbled soft songs, we hypothesized that their transmission qualities would fall in between.

Methods

We conducted a sound propagation experiment using the recorded songs of song sparrows from May 22 to 26, 2015 at three sites near Hartstown, Crawford County, Pennsylvania. The sites were located in typical song sparrow habitat, with males defending territories in and around each site. The experiment entailed playing broadcast songs, crystallized soft songs, and warbled soft songs from a loudspeaker and recording the propagated songs using a calibrated recording system including a measuring microphone. Playback recordings were performed at different heights, along hedgerows and across fields, and at increasing distances between loudspeaker and microphone.

Data availability All data from this study can accessed from the Dryad repository (doi:https://doi.org/10.5061/dryad.68j14).

Test sounds

A set of test sounds was obtained from nine different males during a previous experiment (Anderson et al. 2008). Briefly, we positioned a microphone (Bruel & Kjaer 4145 1″ condenser microphone, Bruel & Kjaer Sound & Vibration Measurement A/S, Naerum, Denmark) with Larson-Davis 2200 pre-amplifier (Larson Davis, Depew, New York, USA) 1 m from a perch, with the height of the microphone matching the height of the perch above the ground. We used playback to lure birds to the perch. Useable recordings were obtained when the bird sang from the perch while directly facing the microphone. We recorded songs onto a Marantz PMD670 digital recorder (Marantz America, Inc., Westbury, NY, USA) (16 bit, 44,100 pts./s sampling rate). Using this setup, all test sounds used to create playback stimuli for the propagation experiment were of high signal-to-noise ratio and were recorded at the same distance to the singing bird.

We selected 18 song exemplars in total to create a standard program of test songs for playback (Fig. 1): 6 broadcast songs, 6 crystallized soft songs, and 6 warbled soft songs, with 1 s of silence between each exemplar and 3 s between each song category. The sample of crystallized soft songs we used were broadcast song types that we recorded when sung at low amplitude; four of these had some of the high-frequency sweeps and low-frequency buzzes common in warbled soft songs (Fig. 1). Figure 2 shows averaged power spectra for the three song categories, showing that the six chosen exemplars of each category had the same general frequency profiles as the much larger sample analyzed in Anderson et al. (2008). In particular, the warbled soft song sample had more energy at lower and higher frequencies compared to the broadcast song sample (see also Fig. 1), with the crystalized soft song sample intermediate. This suggests that the song sample chosen for playback adequately represents the differences in acoustic structure between soft songs and broadcast songs. We modified all songs using Audacity (audacityteam.org) software by applying a low-pass filter (1 kHz) to remove background noise, and normalizing all songs to the same peak amplitude. We then created two versions of the playback file set to different peak amplitudes, 83 ± 2 dB SPL (i.e., re 1 μPa at 1 m) and 63 ± 2 dB SPL, corresponding to natural amplitudes of broadcast and soft song, respectively (Anderson et al. 2008). We confirmed these amplitudes in the field using our playback setup and a Galaxy Audio CM-160 type II sound level meter

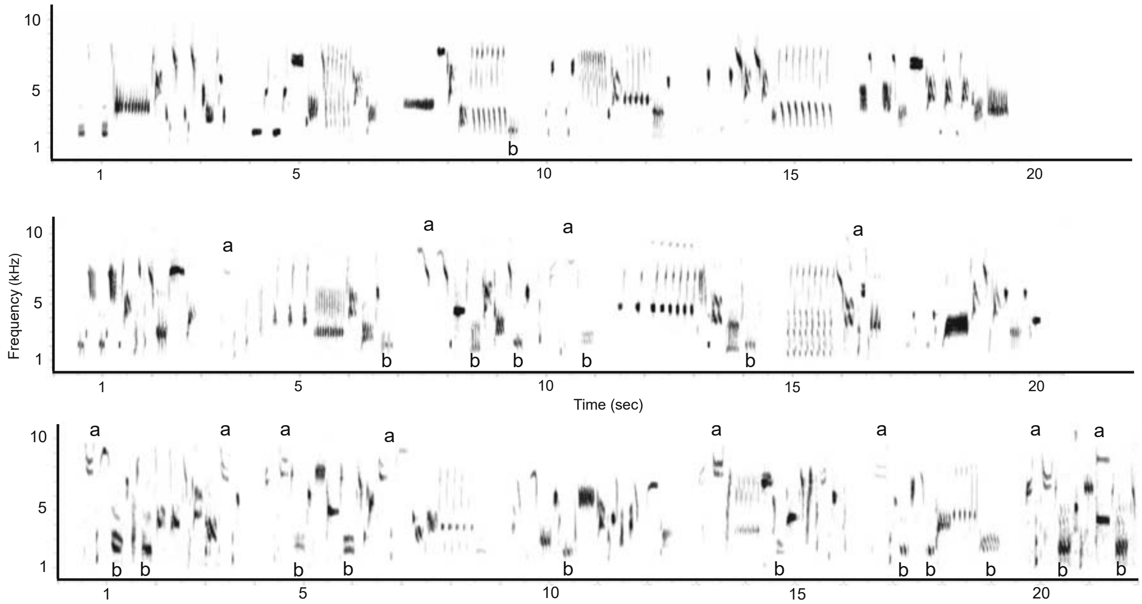

Fig. 1 Spectrograms of the broadcast songs (top row), crystallized soft songs (middle row), and warbled soft songs (bottom row) used in the song propagation experiment. Darker sounds are relatively louder. Warbled soft songs are songs produced at low amplitude that are not present in the broadcast repertoire (i.e., are never given at high amplitude). Crystallized soft songs are songs given at low amplitude that each matches the basic structure of a song type from the broadcast repertoire. Crystallized soft songs often have added notes that are rare in broadcast song but common in warbled soft song, in particular frequency-modulated sweeps at high frequencies (a) and brief buzzes below 2 kHz (b)

held at 1 m from the loudspeaker. At each data collection point, the playback file was played three times at 83 dB SPL and then three times at 63 dB SPL.

Experimental design

The test sound playbacks were broadcast from an Anchor Audio AN-Mini loudspeaker (Anchor Audio Inc., Carlsbad, CA) and re-recorded using a Marantz PMD-660 digital recorder and a calibrated measuring microphone (Larson-Davis 2540 0.5″ free field condenser microphone coupled with a Larson-Davis 2200 pre-amplifier). Files were stored as *.wav* files at a 44.1 kHz sampling rate and 16-bit resolution.

We oriented the playbacks to propagate either along a hedgerow or out into a field (hereafter "habitat"), and at two heights, 1 and 3 m (hereafter "height"), corresponding to typical locations from which song sparrows sing. Propagated sounds were re-recorded first at 1.25 m to serve as models for the acoustic analysis and then at five horizontal distances (hereafter "distance"; 2.5, 5, 10, 20, and 40 m). Within sites,

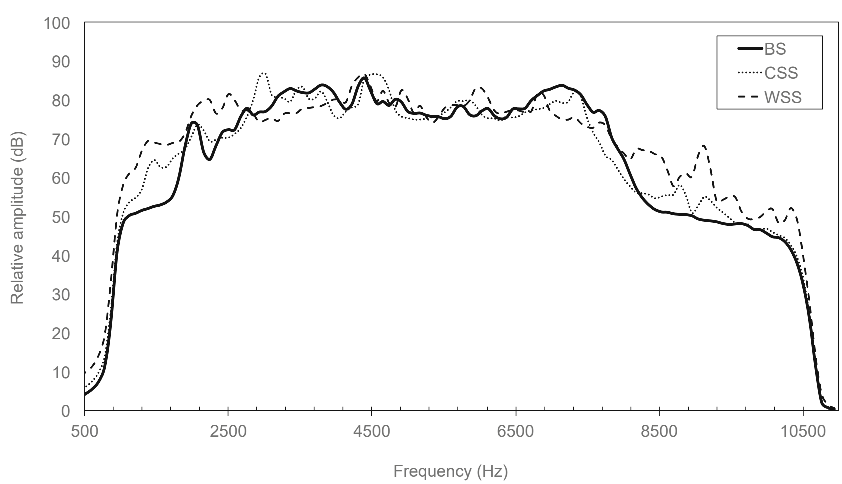

Fig. 2 Averaged power spectra for transmission playback stimuli: broadcast (BS; $n = 6$), crystalized soft (CSS; $n = 6$), and warbled soft (WSS; $n = 6$) songs. Averaged spectra were created in Raven Pro 1.4 and drawn with a 500–11,000 Hz analysis bandwidth, a Hanning window, a 3 dB filter bandwidth of 124 Hz, a 50% overlapped time grid with a hop size of 256 samples, and a DFT size of 512 samples with grid spacing of 86.1 Hz. Amplitudes are expressed in decibels relative to an arbitrary level of 1 and do not represent absolute sound level

we started in the hedgerow habitat with the 1-m height and 2.5-m distance, and then progressed through all distances before repeating those distances at 3-m height. We then repeated the entire series with the playback oriented out into the field. We did not make recordings on days when winds were strong. In the few cases when wind noise was frequent, we re-recorded the transmission playback several times to ensure that we would have at least one recording of each song exemplar that was free of wind noise.

Acoustic analysis

We analyzed the acoustic degradation of the propagated sounds using SigPro 3.25 and an established protocol (Dabelsteen et al. 1993; Holland et al. 2001; Balsby et al. 2003; Rek 2013). Because the test sound playback was repeated three times at each amplitude at each location, there were three recordings of each song exemplar. For analysis, we chose the replicate with the highest matching cross-correlation score between the propagated sound and the model sound ensuring we had the least degraded exemplar for measurements. In total, we analyzed 1944 songs with 1080 songs played at 83 dB SPL and 864 songs played at 63 dB SPL. There were fewer useable songs at the 63 dB SPL amplitude level because songs played at 40 m from the microphone at that amplitude were not detectable on the recordings. We measured four degradation variables over the full length of each song: signal-to-noise ratio (amount of energy in the signal relative to the background noise), tail-to-signal ratio (amount of energy in the tail of echoes of the propagated sound relative to the energy of that propagated sound, using the time window of the model sound for reference as it has an unambiguous endpoint, see Holland et al. 2001), excess attenuation (loss of amplitude in excess of that expected due to spherical spreading), and blur ratio (amount of frequency-dependent distortion in the propagated sound corrected for low signal-to-noise ratio). Excess attenuation is calculated as $EA = -20\log k - A$, where k represents the ratio between propagated sound and model waveforms and A is the attenuation by spherical spreading (6 dB SPL per doubling of distance). We measured the background noise level for each of the 83 and 63 dB SPL levels in a recording from a 1-s pause within the file that did not contain any transient sounds (Rek 2013).

This study did not involve animal subjects. The researcher who analyzed the data (JN) was not present in the field during acoustic data collection and was blind to the field conditions. The acoustic data could not be analyzed using blind methods because the audio files contained song categories that were recognizable to the analyst, but the audio analysis process using SIGPRO was automated to the degree that bias was unlikely.

Statistical analyses

We used linear mixed-effects models (LMM) to test for differential acoustic propagation of the three song categories over distance and to test how height and habitat affected song transmission. We analyzed the 83 and 63 dB SPL recordings using models with different variance-covariance structures because the data for the two playback amplitudes had different distributions. For each playback amplitude, we constructed separate LMMs for the four degradation variables: signal-to-noise ratio, tail-to-signal ratio, excess attenuation, and blur ratio. Each LMM had four fixed factors: song category (broadcast, crystalized soft, warbled soft), habitat (hedgerow and field), height (1 and 3 m), and distance (2.5, 5, 10, 20, and 40 m). We excluded the 40-m recordings from the analysis of the 63 dB SPL playbacks because the songs were not detectable in the recordings at that distance. The songs recorded at the 20-m distance at 63 dB SPL source amplitude were detectable, but these measurements show relatively greater variation and may be less reliable given that most had very low signal-to-noise ratios (< 5 dB SPL).

We included the main effects and two-way interactions between all fixed factors in our analyses. We included site (three sites) as a random factor in all models. Distance was coded as a repeated measure factor with the subject being the unique data point for a particular site, habitat, and height combination. The covariance structure for the residuals was selected using Akaike's information criterion (Akaike 1974). A first-order autoregressive structure (AR1) was used for the 83 dB SPL recordings, and a heterogeneous first-order autoregressive structure (ARH1) was used for the 63 dB SPL. We used post hoc tests for all pairwise comparisons within main effects and all two-way interactions using Tukey's HSD for multiple comparisons. All statistics were conducted in SPSS v24.

Results

When all songs were played at 83 dB SPL, we found no differences between broadcast songs, crystallized soft songs, and warbled soft songs for any of the acoustic transmission measures (Table 1). When played at 63 dB SPL, both forms of soft song had lower blur ratios compared to broadcast songs (Table 2, Fig. 3), but did not differ in the other three measures of transmission. Although we analyzed the two playback amplitudes separately, in general, the largest differences in signal degradation were due to playback amplitude, especially for signal-to-noise and blur ratios.

At both 83 and 63 dB SPL, we found greater degradation at lower heights and farther distances, and interaction effects with habitat (Table 2, Figs. 4 and 5). At both amplitudes, songs played at 3-m height had significantly less excess

Table 1 ANOVA table of the linear mixed-effects models for 83 dB SPL level showing the main effects and interactions of the sound degradation and attenuation variables (SNR = signal-to-noise ratio, TSR = tail-to-signal ratio, EA = excess attenuation, BR = blur ratio). Italic *p* values indicate that post hoc comparisons were significant

	SNR			TSR			EA			BR		
	F	df	*p*	*F*	df	*p*	*F*	df	*p*	*F*	df	*p*
Song category	0.615	2, 200	0.541	1.181	2, 243	0.309	0.247	2, 174	0.781	1.808	2, 316	0.166
Habitat	0.081	1, 200	0.776	2.374	1, 243	0.125	2.063	1, 174	0.153	0.078	1, 316	0.781
Height	2.597	1, 200	0.109	0.227	1, 243	0.634	16.883	1, 174	*< 0.001*	76.437	1, 316	< 0.001
Distance	3747.003	4, 429	*< 0.001*	28.553	4, 244	*< 0.001*	3458.687	4, 339	*< 0.001*	398.880	4, 262	*< 0.001*
Song category × habitat	0.036	2, 239	0.965	0.921	2, 374	0.399	0.022	2, 265	0.979	0.732	2, 272	0.482
Song category × height	0.070	2, 239	0.932	0.729	2, 374	0.483	0.266	2, 265	0.767	0.030	2, 272	0.970
Song category × distance	0.214	8, 429	0.988	1.273	8, 244	0.258	0.110	8, 339	0.999	0.744	8, 262	0.652
Habitat × height	1.266	1, 239	0.262	0.492	1, 374	0.483	27.507	1, 265	*< 0.001*	38.845	1, 272	*< 0.001*
Habitat × distance	37.614	4, 429	*< 0.001*	1.453	4, 244	0.217	23.971	4, 339	*< 0.001*	4.745	4, 262	0.001
Height × distance	26.671	4, 429	*< 0.001*	2.008	4, 244	0.094	25.521	4, 339	*< 0.001*	4.243	4, 262	0.002

attenuation along the hedgerow compared to the field ($p < 0.001$ for both amplitudes; Fig. 4). At 83 dB SPL, songs played at 1-m height had significantly greater blur ratio in the field than along the hedgerow ($p = 0.010$; Fig. 4). At 63 dB SPL, songs played at 1-m height showed significantly decreased tail-to-signal ratio in the field compared to the hedgerow ($p = 0.037$; Fig. 4). For the measures of signal-to-noise ratio and excess attenuation, at both amplitudes, songs propagated along hedgerows degraded significantly less at 10 m (83 dB SPL: $p = 0.003$; 63 dB SPL: $p < 0.001$; Fig. 5) and significantly more at the farthest distances, compared to songs propagated into fields (83 dB SPL, 40 m: $p < 0.001$; 63 dB SPL, 20 m: $p < 0.001$; Fig. 5). For tail-to-signal ratio, songs degraded equally for all distances up to 20 m for both amplitudes and less along the hedgerow at 40 m at 83 dB SPL ($p < 0.001$; Fig. 5). For blur ratio, songs degraded similarly at 83 dB SPL along the hedgerow compared to the field for all distances. At 63 dB SPL, songs showed higher degradation at 10 m along the hedgerow compared to the field ($p < 0.001$), but degraded similarly at other distances (Fig. 5).

Discussion

The eavesdropping avoidance hypothesis makes two predictions related to the acoustic traits of soft sounds: that selection should favor traits in addition to amplitude that reduce the transmission range of soft sounds (Dabelsteen 2005) and that transmission distances of soft sounds should be shorter than broadcast sounds when amplitudes are equalized (Searcy and Yasukawa 2017). The first prediction is supported for warbled soft songs in the song sparrow, which have higher maximum frequencies, lower minimum frequencies, and greater frequency bandwidth, as well as a greater number of notes types, compared to broadcast songs or crystallized soft songs (Anderson et al. 2008). Our results do not support the second prediction: broadcast songs, crystallized soft songs, and warbled soft songs showed similar degradation and attenuation values when played at broadcast song amplitude. When played at soft song amplitude, both categories of soft song transmitted slightly better, not worse, compared to broadcast song, which runs directly counter to the eavesdropping avoidance hypothesis. We observed better transmission of soft songs at low amplitude for only one of the four degradation measures, however, and the differences between song categories were small. Overall, we conclude that the three song categories do not seem to differ in transmission capacity when transmitted at the same amplitude in the same habitat.

Our results differ from a similar study in white-throated thrushes (*Turdus assimilis*), in which soft song syllables degraded and attenuated more than broadcast syllables when both were played at 85 dB SPL (Vargas-Castro et al. 2017). The degree to which soft song differs from broadcast song in the two species provides a proximate explanation for the degradation differences between these two studies. The difference in the frequency range of broadcast and soft syllables is pronounced in the white-throated thrush, with soft syllables being much higher pitched than broadcast syllables. By contrast, the frequency ranges of the soft songs and broadcast songs of song sparrows overlap completely, with warbled soft songs having a broader frequency range on average (Anderson et al. 2008). Although song sparrow soft songs contain elements at higher and lower frequencies than are typically found in broadcast songs, this difference does not appear to lead to different song transmission properties. A possible ultimate explanation for the degradation differences in the two species is that eavesdropping avoidance is more important for signals that are used in courtship as well as aggression, as is true of

Table 2 ANOVA table of the linear mixed-effects models for 63 dB SPL level (excluding 40-m distance) showing the main effects and interactions of the sound degradation and attenuation variables (SNR = signal-to-noise ratio, TSR = tail-to-signal ratio, EA = excess attenuation, BR = blur ratio). Italic *p* values indicate that post hoc comparisons were significant

	SNR			TSR			EA			BR		
	F	df	*p*	*F*	df	*p*	*F*	df	*p*	*F*	df	*p*
Song category	1.809	2, 179	0.167	0.013	2, 335	0.987	0.173	2, 173	0.841	5.467	2, 275	*0.005*
Habitat	2.174	1, 179	0.142	9.424	1, 335	0.002	4.278	1, 173	0.040	4.562	1, 275	0.034
Height	14.362	1, 179	< 0.001	9.255	1, 335	0.003	13.267	1, 173	< 0.001	12.459	1, 275	*< 0.001*
Distance	965.966	3, 222	*< 0.001*	6.074	3, 315	*< 0.001*	886.254	3, 237	*< 0.001*	652.657	3, 275	*< 0.001*
Song category × habitat	0.025	2, 303	0.976	0.479	2, 330	0.620	0.007	2, 302	0.993	1.759	2, 233	0.175
Song category × height	0.070	2, 303	0.932	1.822	2, 330	0.163	0.327	2, 302	0.721	0.005	2, 233	0.995
Song category × distance	0.296	6, 222	0.939	1.296	6, 315	0.259	0.498	6, 237	0.810	1.893	6, 275	0.082
Habitat × height	0.305	1, 303	0.581	4.384	1, 330	*0.037*	46.021	1, 302	*< 0.001*	7.079	1, 233	*0.008*
Habitat × distance	21.181	3, 222	*< 0.001*	3.422	3, 315	*0.018*	8.497	3, 237	*< 0.001*	6.647	3, 275	*< 0.001*
Height × distance	18.795	3, 222	*< 0.001*	3.772	3, 315	*0.011*	5.036	3, 237	*0.002*	9.824	3, 275	*< 0.001*

soft song in white-throated thrushes, than in signals used solely in aggression, as is true of soft song in song sparrows.

Our results add to the growing body of evidence refuting the eavesdropping avoidance hypothesis for soft song in the song sparrow. Production of soft song is expected to increase during territorial intrusions if predation risk is high, yet two experimental studies using conspecific alarm calls (Searcy and Nowicki 2006) or predator calls (Cooper's hawk *Accipiter cooperi*; Akçay et al. 2016) showed decreased use of soft song relative to playbacks of control stimuli. A second prediction is that territory owners that use soft song during agonistic interactions will incur less intrusion by neighboring males. Searcy and Nowicki (2006) found no difference in the duration of neighboring male intrusions compared between trials in which simulated territory owners replied with broadcast songs versus soft songs.

Although we found no consistent or substantial differences in transmission properties among the three categories of song sparrow song, we did find interaction effects among transmission height, habitat, and distance. Our findings are in line with previous studies demonstrating decreased degradation with increased height (Morton 1975; Marten and Marler 1977), increased degradation with increased transmission distance (Dabelsteen et al. 1993), and an interaction between height and distance in their effects on overall degradation (Dabelsteen et al. 1993). Although habitat characteristics have prominent effects on sound transmission (Morton 1975; Marten and Marler 1977), habitat did not emerge as a significant main effect in our models of transmission variables at broadcast song amplitude. Apparently the two habitats we chose, projecting songs along a hedgerow versus out into a field, did not impose the kinds of consistent patterns of increased degradation at lower heights and farther distances (Figs. 4 and 5) shown in other studies. The mixed effects we found could be attributed to variable degradation over the wide frequency range of elements in song sparrow songs (1–10 kHz), as has been seen in previous studies (Morton 1975; Marten and Marler 1977). For example, sounds at 2 kHz show

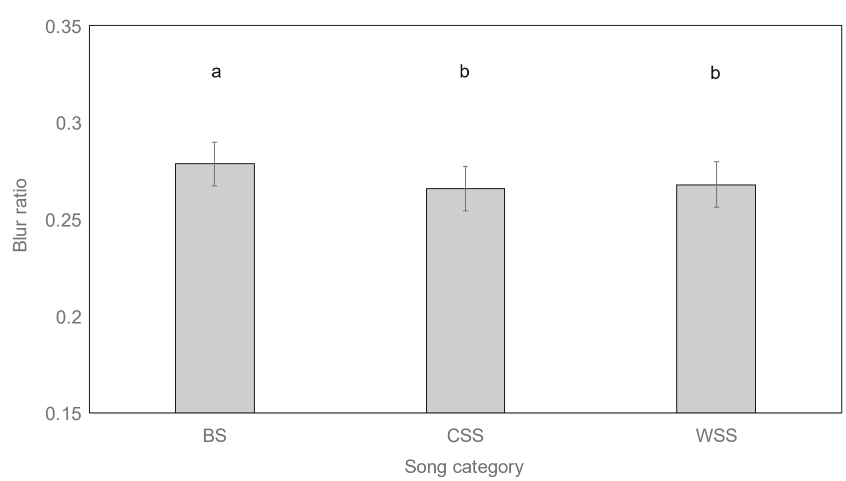

Fig. 3 Differences in blur ratio (mean ± SE) among the broadcast (BS), crystallized soft (CSS), and warbled soft (WSS) song categories played at 63 dB SPL

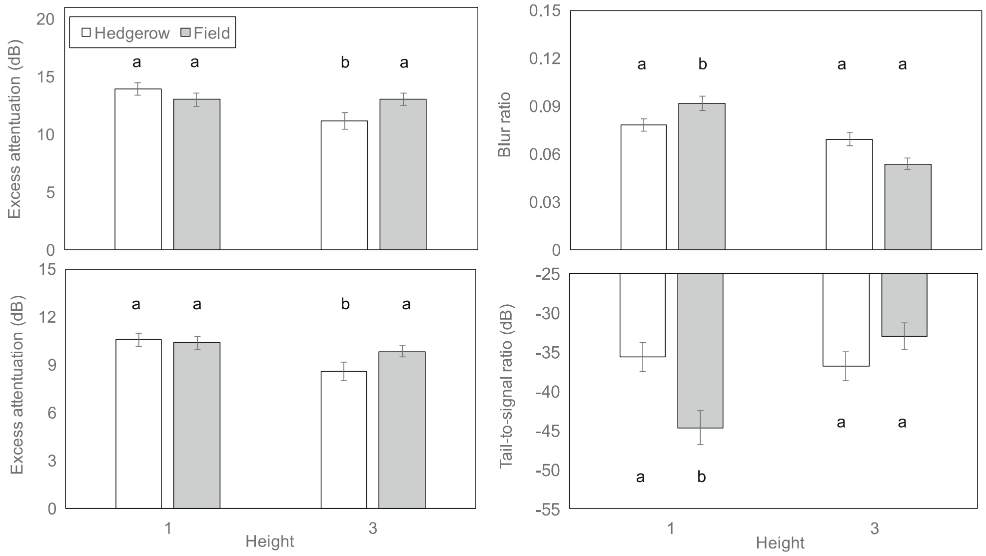

Fig. 4 Mean ± SE difference in excess attenuation and blur ratio in the interaction between habitats and heights (1 and 3 m) at 83 (top) and 63 dB SPL (bottom). Bar colors represent the hedgerow (white) and field (gray) habitats. Statistically significant differences based on post hoc tests are shown with different letters above the bars

less excess attenuation than those at lower or higher frequencies in forest or edge habitats, but show greater attenuation in field habitats (Morton 1975). Many of our sparrow songs had introductory notes at 2 kHz (Fig. 1), and those elements may transmit particularly well along hedgerows.

We found no evidence to support the hypothesis that the acoustic properties of soft songs serve to reduce the transmission range of these aggressive signals. Our results together with those of earlier studies (Searcy and Nowicki 2006; Akçay et al. 2016) seem sufficient to reject the eavesdropping avoidance hypothesis as the explanation for the acoustic properties of soft song in song sparrows. Other explanations must thus be sought for the acoustic features of song sparrow soft song, including its defining feature of low amplitude. One hypothesis is that the properties of soft songs encode different kinds of information than broadcast songs specific to aggressive communication at close range. For example, soft songs might function as a reliable indicator of male quality or fighting ability (Anderson et al. 2008). Soft songs have a wider frequency range due to the high-frequency notes and low-frequency buzzes they contain. Especially in the case of warbled soft songs, birds often alternate quickly between high-

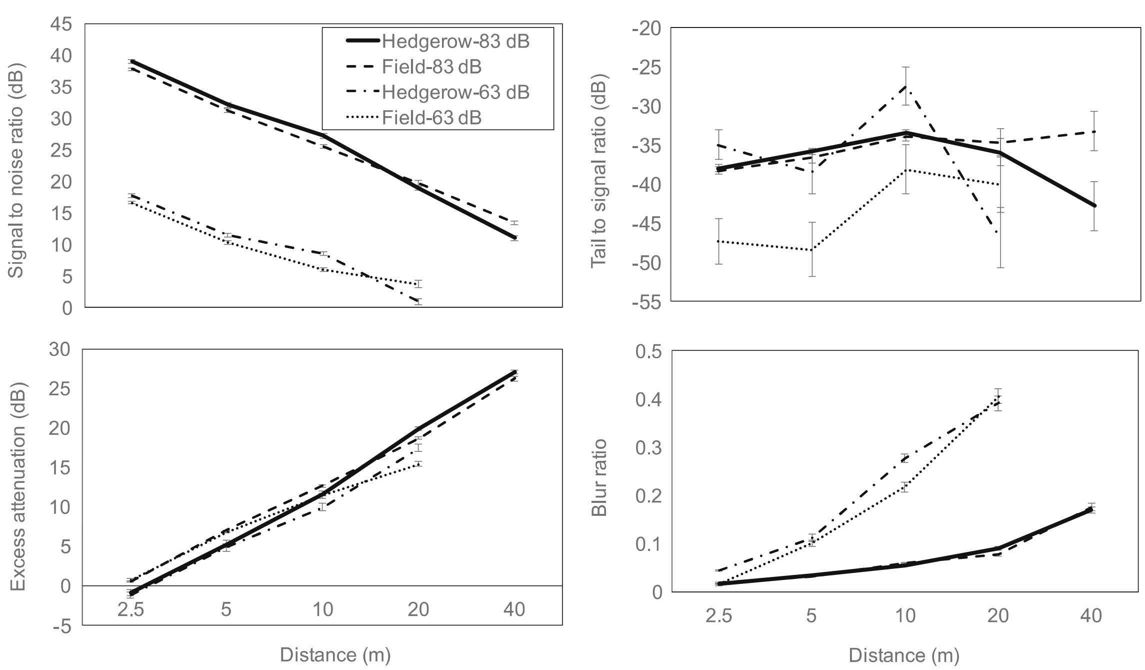

Fig. 5 Mean ± changes in signal-to-noise ratio, tail-to-signal ratio, excess attenuation, and blur ratio across distance for the playbacks in the hedgerow and field habitats. Line types represent the 83 dB SPL, hedgerow (black); 83 dB SPL, field (dashed); 63 dB SPL hedgerow (dot dashed); and 63 dB SPL, field (dotted) habitats at their respective playback levels

and low-frequency elements, which may serve to showcase physical ability. Another possibility is that the acoustic properties of soft song are a consequence of a bird readying itself to fight. The "readiness hypothesis" (Akçay et al. 2011; Akçay and Beecher 2012) is a physical constraint explanation for soft song: preparing to fight (visually tracking the opponent, protecting against attack) conflicts with the bill and head movements used to produce broadcast song, including opening the bill wide and arching the head back. Future studies could test these hypotheses by examining the relationships between soft song acoustic structure and indices of male quality such as mass, age, or aggressiveness and by testing for the predicted trade-offs between loud singing and bill and head position.

An alternative explanation for the greater variability of soft song, in particular warbled soft song, is that this variability counters the utility of eavesdropping. Our data suggest that song sparrow soft song lacks acoustic structures that reduce sound transmission, thereby reducing the risks of eavesdropping. Soft songs are, however, less stereotyped and more variable in note composition compared to broadcast song (Anderson et al. 2008). This increased variability may reduce the ability of receivers to identify a softly singing individual, which in turn may reduce the utility of the information gained through eavesdropping (Dabelsteen 2005). This idea leaves open the possibility that the eavesdropping avoidance hypothesis can be applied to song sparrow soft song if a high degree of variation counters the utility of eavesdropping through anonymity.

Acknowledgments We thank Caitlin Cantrell for help with field work. We thank Florida Atlantic University for funds to RA and the Duke Office of the Provost for funds to SN. Access to field sites was granted by the Pennsylvania State Game Commission, and logistical support in the field was provided by the Pymatuning Laboratory of Ecology of the University of Pittsburgh. We also thank two anonymous reviewers whose suggestions improved the manuscript.

Compliance with ethical standards

Ethical approval Our study did not involve animal subjects, only playback and recording of audio that had been collected in a previous study.

Conflict of interest The authors declare that they have no conflict of interest.

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