Soft Song in Song Sparrows: Acoustic Structure and Implications for Signal Function

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Abstract

In many species of songbirds, males sometimes produce songs at distinctly lower amplitude than in normal singing. Depending on the species, these 'soft songs' may be sung in the context of female courtship, male–male aggression, or both. In song sparrows, males produce soft songs during aggressive interactions with other males, and the amount of soft song produced is the only singing behavior that can be used to reliably predict a subsequent attack by the singer. Although soft song is clearly an important signal in this species, little is known about the acoustic structure of soft song or about how that structure compares to the structure of normal 'broadcast song'. We recorded a large sample of soft songs and broadcast songs from 10 male song sparrows, and measured song amplitudes in the field while controlling the subject's distance to a calibrated microphone. We show that song sparrow males produce songs over a wide range of amplitudes, with soft songs in the range of 55–77 dB sound pressure level and broadcast songs in the range of 78–85 dB. We present evidence for two types of soft song: 'crystallized' soft songs that are broadcast repertoire song types sung at low amplitude, and 'warbled' soft songs that are not found in the broadcast repertoire. Although highly variable, warbled soft songs produced by individual birds could be grouped into song types based on spectrographic similarity. To our knowledge, a distinct repertoire of soft song types has not been previously reported for any songbird.

Introduction

Male songbirds are known for their conspicuous broadcast songs. In most songbird species, broadcast songs are produced at high amplitudes such that their active space (the distance from a sound source over which a signal is detectable) extends well beyond territorial boundaries (Brenowitz 1982; Wiley & Richards 1982; Dabelsteen et al. 1993; Holland et al. 1998; Naguib & Wiley 2001). In addition to broadcast songs, songs of low amplitude, variously termed 'quiet song', 'twitter song', 'whisper song' or 'soft song,' have been noted for some songbird species. Examples include the European blackbird *Terdus merula* (Dabelsteen 1984; Dabelsteen & Pedersen

1990), the European robin *Erithacus rubecula* (Lack 1965; Dabelsteen et al. 1997), the dunnock *Prunella modularis* (Snow 1988), the alpine accentor *Prunella collaris* (Langmore et al. 1996), the dark-eyed junco *Junco hyemalis* (Titus 1998), and the whitethroat *Sylvia communis* (Balsby 2000; Balsby & Dabelsteen 2002). Morton (2000) notes personal observations of 'whisper song' in 24 species of North American passerines. Soft song has not been closely studied in most species; hence the contexts in which soft songs are produced, as well as their signal value, remain poorly understood. The best studied cases are low-amplitude 'twitter song' in the blackbird (Dabelsteen 1984; Dabelsteen & Pedersen 1990), and 'short-range song' in the dark-eyed junco (Titus

1998). Both are given at close range by males that are courting females or threatening rival males (Dabelsteen & Pedersen 1988, 1990). Accounts of soft song in other species suggest that it occurs primarily at close range during both intra-and inter-sexual interactions (reviews in Dabelsteen et al. 1998; Morton 2000).

Soft song is often described as 'different in acoustic structure' compared with full song (e.g. Dabelsteen et al. 1998), but analyses of soft song acoustic characteristics are scarce because of the inherent difficulty in capturing good recordings of low-amplitude signals. Here we present a detailed acoustic analysis of soft song in the song sparrow (Melospiza melodia), a North American passerine that has been the focus of studies of vocal development and signal evolution for over 50 years.

Male song sparrows have broadcast repertoires of five to 16 distinct song types. Each song type is composed of two to five phrases (trills or note complexes), and a variety of note types (Borror 1965; Mulligan 1966; Podos et al. 1992). Songs generally begin with a trill (repetitions of a syllable), followed by alternation of trills and note complexes that form a unique phonology. Young males crystallize their song-type repertoires during their first year (Marler & Peters 1987) and do not modify their repertoire size or song-type structure after this time (Nordby et al. 2002). Song types are sung in bouts with 'eventual variety' (i.e. AAAAA BBBBB CCCCC). Variants of a given song type are sung within bouts, with changes in the number of syllable repetitions in trills, and with minor additions and deletions of notes. However, within-song type variation is considerably lower than between-song type variation (Stoddard et al. 1988; Podos et al. 1992; Nowicki et al. 1999; Peters et al. 2000).

In addition to broadcast song, song sparrow males sing soft song during aggressive interactions with other males. Preliminary observations suggested that song sparrows produce two types of soft song: low-amplitude versions of broadcast repertoire song types and highly variable 'warbled' songs, a seemingly unstructured series of notes and phrases (Anderson et al. 2007). Soft song has been briefly mentioned in accounts of male–male territorial behavior in song sparrows (Nice 1943) and has been used in composite measures of aggressive response in playback experiments (e.g. Beecher et al. 2000; Burt et al. 2001). Recently, the amount of soft song produced was shown to be the only singing behavior that reliably predicts whether the singer will attack a conspecific mount, suggesting that soft song functions as

a strongly aggressive signal in this species (Searcy et al. 2006).

Soft song in other species has been described as 'whisper-like' or 'much lower in amplitude' compared with broadcast song, but calibrated amplitude measurements have not to our knowledge been made for any species. Accurate measurement of signal amplitude requires: (i) using a calibrated measuring microphone; (ii) controlling for the signaler's distance to the microphone; and (iii) controlling for the signaler's orientation relative to the microphone. One goal of this study was to make field measurements of amplitudes of both soft song and broadcast song in song sparrows that met these three criteria.

The low amplitude of soft song makes it a puzzling signal for use when threatening or intimidating rivals. This apparent disparity between signal form and function, and the seemingly unique acoustic structure of soft song, make it a compelling behavior for further study. Knowledge of soft song acoustic characteristics, and the identification of consistent differences between soft song and broadcast song structure, may provide insights into the information that soft song conveys. Understanding the informational value of soft song may, in turn, help elucidate how soft song functions as a signal. To this end, the primary aim of this study was to describe the acoustic structure of soft song, and compare this structure to normal broadcast song.

Methods

Song Sample

Broadcast songs and soft songs were recorded from each of ten males that were part of an aggressive signaling experiment ('playback recordings') conducted between May and July 2002 and 2003, in Crawford County, Pennsylvania (see Searcy et al. 2006). During these trials, a Nagra DSM loudspeaker was placed face-up on the ground well within the territory of the subject male. On top of the speaker was a taxidermic mount of a song sparrow, in a natural perched pose. A single song sparrow song was played at 10-s intervals for 1 min at the start of the trial, and for 1 min after the mount was revealed. The subject male's songs were recorded using two microphones attached to a Sony TC D5M stereo tape recorder (Sony Corporation of America, New York, NY, USA). One microphone (Realistic omnidirectional, model 33-1070; Radio Shack, a Division of Tandy Corporation, Fort Worth, Texas, USA) was placed 15 cm from the mount. Males often

approached the mount while singing soft songs, allowing us to obtain many recordings with an excellent signal-to-noise ratio. The second microphone (Realistic omnidirectional in a Sony PBR 330 parabola) was held by an observer (SN) who stood approx. 15 m from the speaker/mount setup. Recordings made by this microphone were used in instances where the subject's broadcast songs were overloaded on the mount microphone track (i.e. when the subject was close to the mount). The subject male's songs were recorded throughout the 20-min trials, except for one bird that attacked the mount after 13 min, thus ending the trial. A second observer (WAS) narrated the subject's behavior throughout the trial, and categorized each song by ear as loud or soft based on whether or not the amplitude appeared to be in the range of normal, broadcast song or below that range.

In addition to playback recordings, broadcast song repertoires for each of the test subjects were recorded while they sang undisturbed on their territories (repertoire recordings). Repertoire recordings were made at a distance of 15–20 m from the bird using a Realistic omnidirectional microphone in a Sony PBR 330 parabola. All recordings were made during 06:00–10:30 hours, at least 48 h after a subject's playback trial was completed. Each male's repertoire was considered to be fully recorded once 300 songs were obtained; previous work has shown that new song types are rarely recorded after 200 songs (Searcy et al. 1985; Podos et al. 1992; Hughes et al. 1998).

Song Analysis

We first determined the complete song-type repertoire for each of the 10 subject males using repertoire recordings. We digitized all songs (44 100 pts/s) and made spectrograms (256 pt FFT (Fast Fourier Transform); high-pass filtered at 500 Hz) using the Syrinx sound analysis software (John Burt, http://www.Syrinx-PC.com). The songs sung by each male were then sorted into song types (by RCA) based on visual assessment of spectrographic similarities. Two songs were classified as the same song type if they shared at least one half of their notes or phrases (Beecher et al. 1996, 2000; Hughes et al. 2007). We did not consider syllable repetitions within a trill, nor the strict ordering of notes, when classifying song types. In practice, songs classified to be of the same type shared the majority of their notes and phrases, differing mainly at the end with minor deletions and substitutions of notes and phrases (see Podos et al. 1992).

With the full song-type repertoires determined for each subject, we then classified the songs recorded during each male's playback recording as to whether or not each was a song type from the male's known broadcast repertoire. Here again, we classified two songs as the same song type if they shared at least half of their notes or phrases. As song-type classification by visual inspection of spectrograms is subjective, two observers (RCA and SP) independently performed the same analysis and were blind to each other's repertoire assessments until both were completed.

Song Amplitude Measurements

All amplitudes are given as sound pressure level (SPL) in decibels (dB), and the unit 'dB SPL' refers to the standard reference of dB referenced 20 μPa measured at 1 m (roughly the threshold of human hearing at 1000 Hz; Fay 1988). To obtain calibrated amplitude recordings of song sparrow songs, we provoked males (n = 12; different males than those recorded during the playback experiments) to sing by placing a taxidermic mount of a song sparrow on their territory and broadcasting conspecific songs. We placed the mount and playback speaker near a hedgerow, 60–75 cm off the ground. This position corresponds to the majority of aggressive singing and signaling behaviors observed in previous experiments (Searcy et al. 2006). We positioned a calibrated measuring microphone (Bruel & Kjaer 4145 1″ condenser microphone (Brüel & Kjaer Sound & Vibration Measurement A/S, Naerum, Denmark) with Larson-Davis 2200 pre-amplifier (Larson Davis, Depew, New York, USA)) precisely 1 m from a perch where we had observed the subject bird sing. The height of the microphone precisely matched the height of the perch above the ground. Usable data were obtained when the bird sang from the perch while directly facing the microphone (near 0° incidence). We recorded songs onto a Marantz PMD670 digital recorder (Marantz America, Inc., Westbury, NY, USA) (16 bit, 44 100 pts/s sampling rate). We also recorded calibration tones of known frequency (1 kHz) and amplitudes (94 and 114 dB SPL; GenRad 1987 'Minical' sound level calibrator; GenRad Inc., Westbury, NY, USA) at the beginning and end of every amplitude recording session, and in the case of long sessions (>1 h), in the middle as well. We checked the standards of the GenRad 1987 calibration tone generator against an independent tone generator, a GenRad 1567 (114 dB SPL, 1 kHz).

To measure song amplitudes, we first high-pass filtered (625 Hz) digitized signals to remove extraneous low-frequency environmental noise (mostly wind noise). We then determined amplitudes using the sound pressure level function ('slm' command) in SIGNAL 3.1 (Engineering Design, Berkeley, CA, USA). We used the calibrating signals recorded during a given session to normalize song amplitudes to dB SPL. That is, the voltages of the calibrated tones were known to correspond to 94 dB SPL or to 114 dB, SPL, and this correspondence allowed conversion of the known voltages of the recorded songs to amplitude in units of dB SPL. SIGNAL 3.1 allows SPL levels to be calculated using both fast averaging (125 ms) and slow averaging (1000 ms): we report both measurements.

As described previously, songs in the playback recordings were classified in the field as 'loud' or 'soft' by a single observer (WAS). The consistency of the observer in making these classifications has been supported independently by tests using playback of songs of known amplitude (reported in Searcy & Nowicki 2006). As a further test, we made calibrated field recordings of 81 songs from five males while WAS simultaneously classified the songs as broadcast or soft. The amplitudes of these songs were subsequently determined as described above and compared with the classification made initially in the field.

Measurement of Song Characteristics

We made measurements of seven standard acoustic variables for all songs in order to describe the acoustic features of soft song, and to compare soft song with normal broadcast song. We amplitude-normalized all digital song files in SIGNAL 4.1 by scaling the amplitude of each file to a peak of 0 dB SPL. We then normalized digital spectrograms for onscreen viewing by setting the gray scale to near zero. Individual song measurements were made using on-screen time and frequency cursors. Frequency measurements were made from spectrograms using a 512-pt FFT (resolution = 49 Hz) and time measurements were made from spectrograms using a 128-pt FFT (resolution = 5.1 ms). We defined a note as a continuous spectrogram trace and, following the methods of Podos et al. (1992), defined note types as notes that shared identical or nearly identical spectrographic shape (time–frequency characteristics). We did not consider small variations in note duration and/or frequency characteristics when classifying note types within a song.

For each song we measured: (i) the total number of notes, (ii) the number of note types, (iii) the ratio of total notes to number of note types (note variability index), (iv) maximum frequency (Hz), (v) minimum frequency (Hz), (vi) overall song bandwidth (Hz), and (vii) song duration (ms) (Table 1). In most cases we made measurements on multiple exemplars of each song type (mean = 5 exemplars; range 2–23) for each bird. We performed statistical comparisons of song measurements using the average measurements for each bird; thus the sample size for each category of song is the number of birds in the sample (10) rather than the number of songs in each category.

We entered the seven univariate measures into a principal components analysis and compared the first two principal components (eigenvalues >1) across song categories. We also made univariate comparisons of song measurements to further parse the acoustic differences among broadcast song and soft song. We used the Friedman test, followed by pairwise comparisons using the Wilcoxon matched-pairs signed-ranks test with Dunn-Sidak adjustment of alpha for multiple comparisons ($\alpha = 0.017$). We used non-parametric tests because most song variables did not have similar variances across song categories, and could not be sufficiently normalized using standard data transformation procedures. All statistical tests were performed using SYSTAT 11 (SYSTAT Software Inc., Chicago, IL, USA, 2004).

Results

Broadcast Repertoires

The mean and median repertoire size for broadcast repertoires was eight song types (range: 6–10). A mean of 335 songs (range: 270–492) was recorded from the 10 subjects. Our goal was to record at least 300 songs from each bird to be certain that we had exemplars of the entire song repertoire. We did not meet this criterion for one bird, from which we recorded only 279 songs. We are fairly confident that we recorded the entire repertoire for this subject, however, because multiple authors have found that new song types are rarely discovered after 200 recorded songs (Searcy et al. 1985; Podos et al. 1992; Hughes et al. 1998).

Song Amplitude

We made calibrated field recordings of 326 songs from 12 territorial males. The songs ranged in ampli-
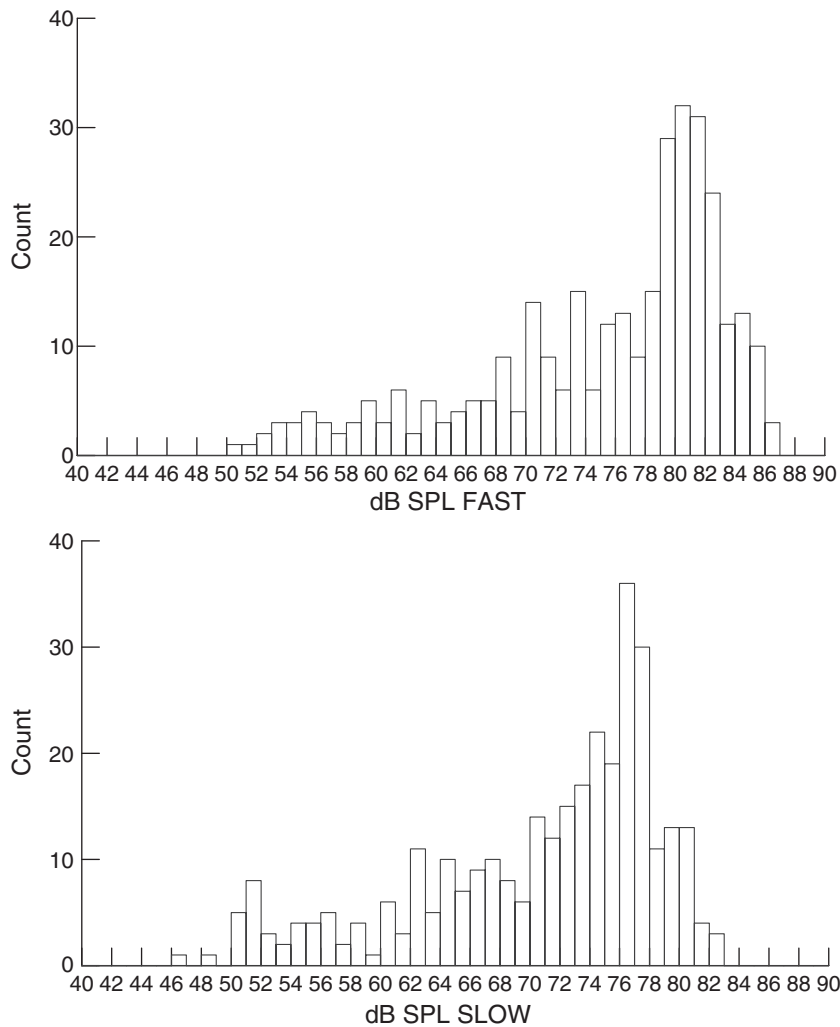
Fig. 1: Distribution of song amplitudes recorded in the field. Songs were recorded from 12 male song sparrows (N = 326 songs) as they sang 1 m from a calibrated measuring microphone.

tude from 50 to 86 dB SPL (mode = 80, median = 78) measured on fast setting (Fig. 1a), and 46 to 80 dB SPL (mode = 76, median = 73) measured on slow setting (Fig. 1b). We found that songs were produced in a relatively continuous range of song amplitudes, without an obviously bimodal distribution of loud vs. soft. This pattern holds for song amplitudes recorded from individual birds; individuals produced songs at a range of song amplitudes, rather than songs that were well clustered into loud and soft categories (data not shown).

In addition to calibrated field recordings, a subset of 81 songs recorded with a measuring microphone (amplitude range 54–85 dB SPL) was classified by ear in the field as loud or soft by a single observer (WAS) who also classified the songs recorded during playback trials (below). The observed subjective cutoff between songs reported as either loud or soft

was 77 dB SPL (Fig. 2), and given this cutoff, the consistency in classifying songs was quite high. All songs (59/59) with amplitudes at 78–85 dB SPL were classified subjectively in the field as loud, and 95% (21/22) of songs at 54–77 dB SPL were classified as soft. The loudest song we measured was 36 dB louder than the softest. An increase of 6 dB SPL equals a doubling in sound pressure (root-mean-squared average amplitude), so a difference of 36 dB SPL equates to the softest soft songs being more than 32 times softer than typical loud broadcast song ($2^5 = 32$) in terms of sound energy. Humans are generally shown to perceive an increase in 10 dB as a doubling in perceived intensity; thus soft song would sound more than eight times softer than broadcast song ($2^3 = 8$) to a human observer (Macmillan 1990). Birds and humans both perceive sound intensity according to
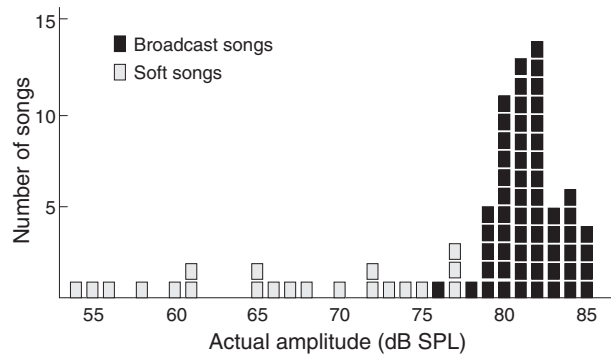
Fig. 2: Calibrated amplitudes of 81 songs labeled as 'broadcast' or 'soft' by an observer (WAS). As calibrated recordings were made in the field, the observer classified each song by ear as a broadcast song or soft song.

Weber's law, i.e. the logarithmic decibel scale, although birds are less sensitive to relative changes in intensity than humans (Dooling & Saunders 1975; Heinz et al. 1980; Okanoya & Dooling 1985; Dooling et al. 2000).

Spectrographic Classification of Playback Songs

We recorded 753 songs from 10 males during playback trials. These songs were classified in the field as 'soft' or 'loud'. The songs were subsequently categorized in the laboratory as belonging to the broadcast repertoire or not, based on whether their spectrograms matched a song type recorded later from the same individual during undisturbed singing. Two independent observers (RCA and SP) agreed on judgments of matching for 98% of the 753 songs. Of the 305 songs classified in the field as loud, 299 (98%) matched a song in the broadcast repertoire and six (2%) did not. Of the 442 songs classified in the field as soft, only 235 (53%) matched a song in the broadcast repertoire; we term this category 'crystallized soft songs'. The remaining 207 soft songs (47%) did not match any song type in the broadcast repertoire; we term this category 'warbled soft song' because of its relatively more variable acoustic structure (see below). The six loud songs that were not judged to belong to the broadcast repertoire actually in each case strongly resembled a broadcast song type, but did not meet the criterion of sharing at least 50% of notes and phrases. These six songs were likely extreme variants of these broadcast repertoire songs (Podos et al. 1992), rather than song types missed during repertoire recordings.

Phonology and Descriptive Features of Soft Song

As we have defined in this study, crystallized soft songs (Fig. 3, center column) are song types from the broadcast repertoire (Fig. 3, left column) sung quietly: they share note composition and syntax with broadcast song types, and are fairly stereotyped, though not invariant. Similar to broadcast song types, the majority of crystallized soft songs follow the general pattern of an introductory trill, followed by alternating trills and note complexes. Warbled soft songs (Fig. 3, right column), by contrast, do not have the stereotyped syntax of alternating trills and note complexes common to broadcast song and crystallized soft song. Instead, warbled soft songs contain few or no trills, and are comprised of alternating note complexes and buzzes.

In addition, soft songs are characterized by distinctive note types that are uncommon in broadcast songs. Warbled soft songs contained multiples of these notes throughout, while they were typically appended to the beginning or end of crystallized soft songs, and were rare or absent in broadcast songs. For example, a high-frequency downswept note (note type 'a', Fig. 3) was present in 61% of warbled soft songs and 39% of crystallized soft songs but only 6% of broadcast songs. Seventeen percent of warbled soft songs contained two or more of these notes, compared with only 8% of crystallized soft songs. A second example is a high-frequency (8–10 kHz) 'double-U' shaped note (note type 'c', Fig. 3) that was present in 96% of warbled soft songs, and 21% of warbled soft songs contained multiples of these notes. The note was present in 64% of crystallized soft songs, but only 10% of the songs contained more than one of these notes. The note was rare in broadcast songs, appearing in only 5%. A final example is a brief low-frequency buzz at approximately 2 kHz (note type 'b', Fig. 3) that was present in 76% of warbled soft songs, with 58% containing more than one such buzz. Seventy-three percent of crystallized soft songs contained at least one buzz, but only 13% contained two or more. Low-frequency buzzes are present in loud broadcast songs but less commonly than in soft songs; 58% of broadcast songs contain buzzes, but of these songs, 71% include only a single buzz.

In many cases, the warbled soft songs produced by a given bird, even though relatively more variable, could be grouped into types. We applied the same criteria used to group broadcast songs into repertoire song types (i.e. sharing of at least 50% of notes, with similar ordering of shared notes and phrases) and
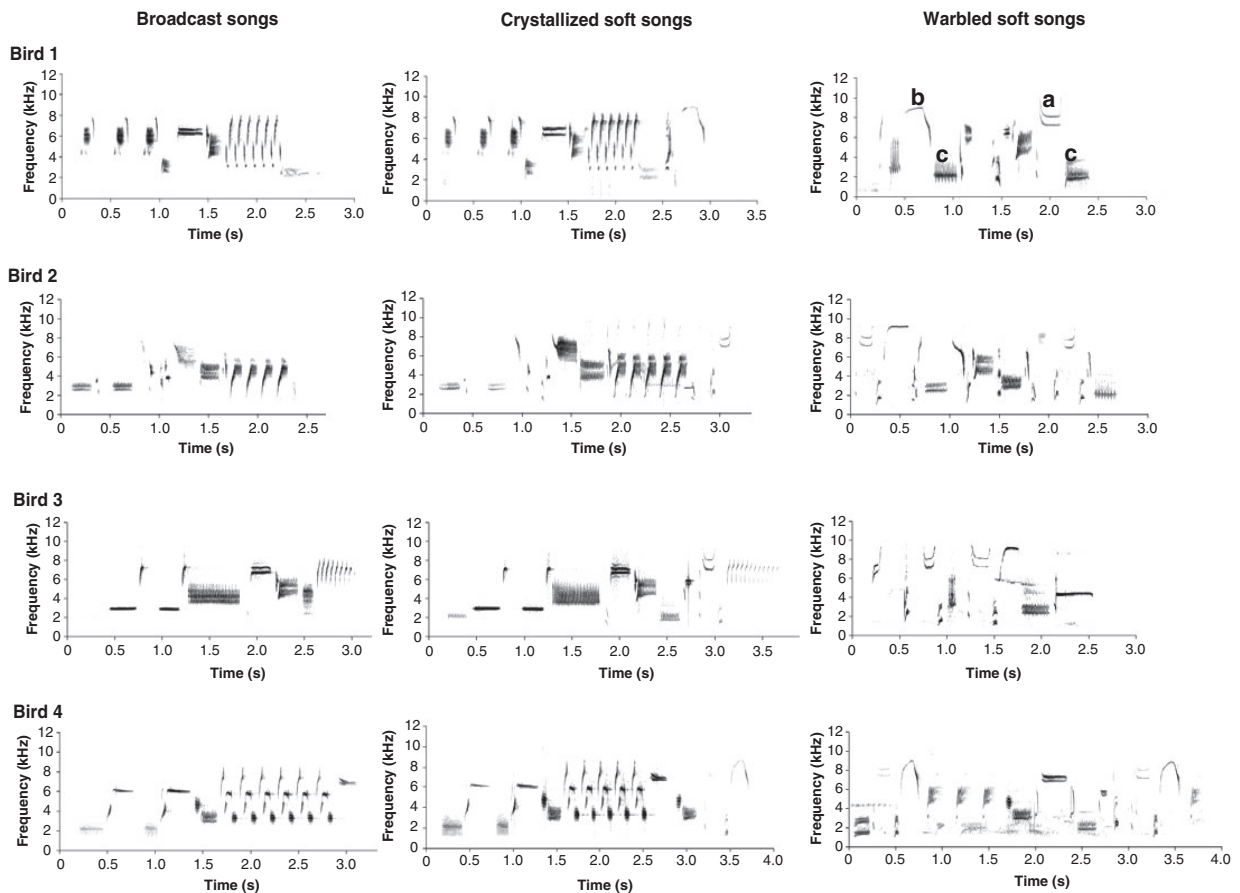
Fig. 3: Examples of broadcast repertoire songs, crystallized soft songs, and warbled soft songs recorded from four male song sparrows. Warbled soft songs are characterized by frequency-modulated sweeps at high frequencies (>8 kHz) ('a' and 'b'), alternated with brief buzzes at or below 2 kHz ('c'). These elements also appear in some crystallized soft songs, usually appended to the end, but are uncommon on broadcast songs.

found that 169 of the 207 (82%) warbled soft songs sufficiently matched other warbled song exemplars and could be grouped as a song type (Fig. 4). The 10 subject birds had a mean of 2.5 warbled soft song types (range 1–5 song types). Soft songs classified as the same type were most often performed in bouts (several repetitions of the same type), in much the same way that broadcast song types are sung. However, in some cases, warbled soft songs were sung alternating with broadcast songs (Fig. 5), or with crystallized soft songs.

Finally, we found that the majority of the very lowest amplitude songs were warbled soft songs. From the set of calibrated songs for which we had amplitude measures, we took 142 songs with amplitudes ≤77 dB SPL (fast setting) and categorized each as a crystallized soft song or warbled soft song (Fig. 6). The majority of the softest songs were categorized as warbled soft songs: 24 of 32 warbled soft songs (75%) were ≤60 dB SPL, while only five of 110 (4.5%) crystallized soft songs were ≤60 dB SPL.

Principal Components Analysis of Song Features

Multivariate analysis generated two principal components that explained greater than 74% of the variance in measured acoustic characteristics of broadcast song, crystallized soft song, and warbled soft song. The first principal component (PC1) explained 57% of the variance in song measurements, and six of the seven song measures loaded heavily on this index (Table 2). Positive loadings on PC1 reflect songs with more notes, longer duration, and higher minimum frequency. Negative loadings reflect larger note variability, higher maximum frequency, and a wider frequency range. PC2 explained 17.5% of the variance in song measurements. The number of note types per song loaded heavily and positively on PC2; thus PC2 reflects songs comprised of a larger number of note types.

The 95% confidence ellipses for PC1 and PC2 factor scores show that these principal components separate warbled soft song from both crystallized soft
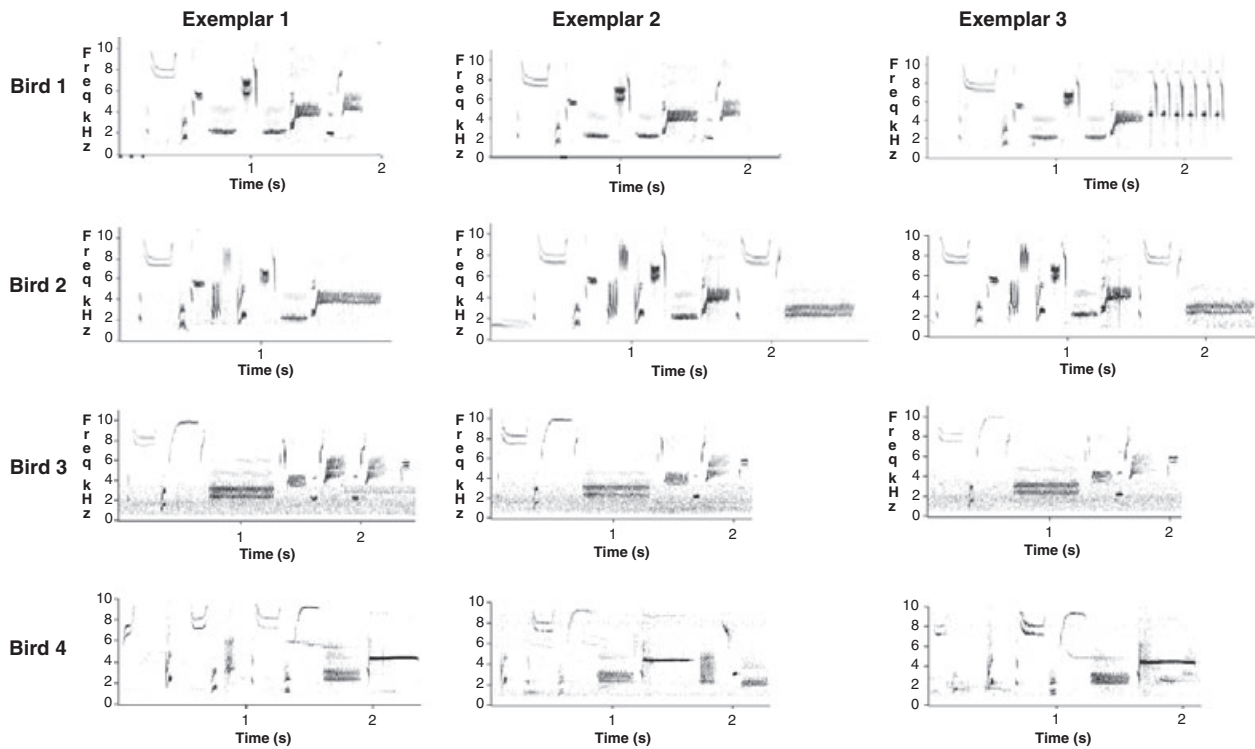
Fig. 4: Exemplars of warbled soft song types recorded from four subject birds. As is the case with broadcast song, exemplars within a given song type are not identical, but do share a large proportion of notes, with notes sung in roughly the same order.
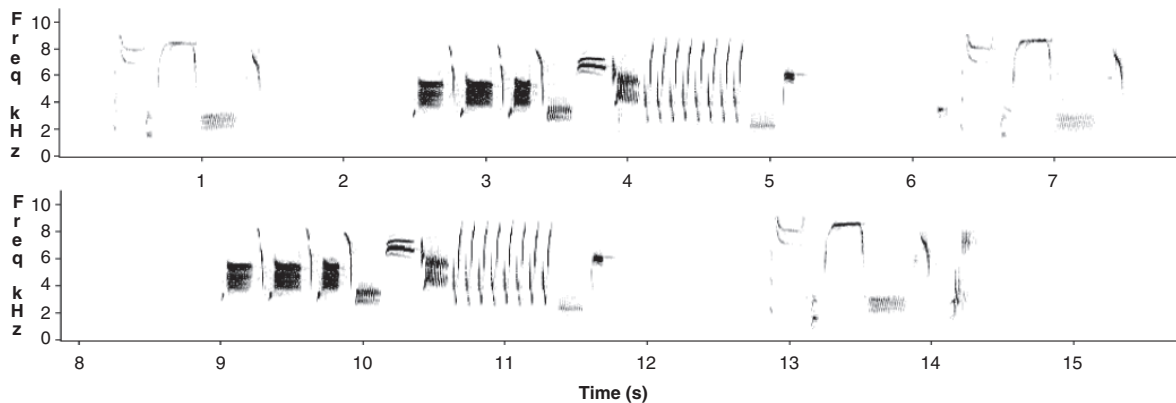

Fig. 5: Example of a study subject singing warbled soft songs alternated with broadcast songs. Silent periods between songs have been cropped in order to fit the song sequence on two lines.

song and broadcast song (Fig. 7). By contrast, there is not a clear separation between crystallized soft song and broadcast song. This result was expected given that, by definition, crystallized soft songs are essentially broadcast song types sung quietly. Nonetheless, there are acoustic differences between crystallized soft songs and broadcast songs, particularly in PC1 song measures.

We used PC1 factor scores (score coefficients multiplied by standardized measurements) to collapse the six song variables into one index that could be compared across song categories. The three song categories differed significantly on the song features that comprised PC1 (Friedman test: $Q = 18.200$, $p = 0.000$, 2 d.f.). Post hoc pair-wise comparisons (Wilcoxon tests) of PC1 across the three song categories showed that each pair of song categories differed significantly (broadcast vs. warbled $Z = -2.8$, $p = 0.005$; crystallized vs. warbled $Z = -2.7$, $p = 0.007$; broadcast vs. crystallized $Z = -2.9$, $p = 0.003$).
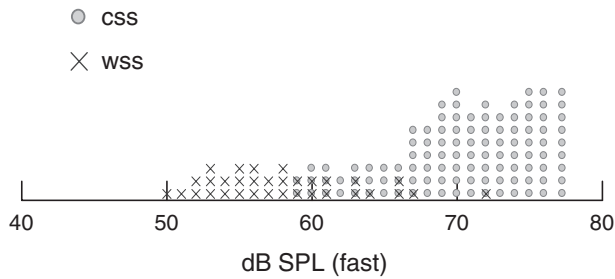
Fig. 6: A density plot showing the relative amplitude distributions of warbled soft songs and crystallized soft songs. This sample of 142 soft songs (≤77 dB SPL) is a subset of the calibrated song recordings (326 songs). Complete song type repertoires were not available for all birds in this sample, thus we could not be certain for this subset that soft songs were part of the bird's repertoire (CSS) or not (WSS). However, the unique phonology of warbled soft songs makes them quite distinct in most cases. We included here only songs that could be categorized as warbled or crystallized with good confidence.

A Friedman test comparing PC2 factor scores (PC2 reflects the number of note types per song) across the three song categories was not significant (Q = 2.400, p = 0.301, 2 d.f.).

Univariate Comparisons of Acoustic Measures

For two of the seven univariate acoustic measures, number of note types and song duration, we found no significant variation across the categories of broadcast song, crystallized soft song, and warbled soft song (Table 2). The remaining five measures showed significant variation across the three categories, and for these measures we performed post hoc tests of differences between pairs of categories. On two of these five measures, the number of notes and note variability, crystallized soft songs were not distinguishable from broadcast songs, and both differed significantly from warbled soft songs (Table 2).

Table 2: Eigenvalues and factor loadings for principal components analysis of song measures from broadcast song (n = 299), crystallized soft song (n = 235), and warbled soft song (n = 207)

Song measure	Principal component	
	1	2
No. notes	0.885	0.167
No. note types	0.391	0.855
Note variability (note types/notes)	−0.832	0.304
Minimum frequency	0.785	−0.150
Maximum frequency	−0.850	0.225
Frequency range	−0.728	0.328
Song duration	0.721	0.441
Eigenvalue	4.018	1.227
% Variance explained	57.404	17.523

Principal components 1 and 2 had eigenvalues greater than 1.0.

For the three spectral measures, minimum frequency, maximum frequency, and frequency range, the categories of broadcast song and warbled soft songs were most different, with crystallized soft songs intermediate (Table 2). Spectral differences can be visualized by comparing averaged power spectra of the three song categories. We created power spectra in SIGNAL 4.1 for the songs classified as broadcast, crystallized, and warbled, and averaged the power spectra within each song category (Fig. 8). On average, warbled soft songs have greater energy at both low frequencies (1–2 kHz) and high frequencies (9–10 kHz) compared with broadcast songs, with crystallized soft songs intermediate.

In addition to differing in average values from the other two categories of song, warbled soft songs tended to be more variable in some acoustic measurements. Warbled soft songs were more variable in the number of notes they contained, with some songs containing many notes and others containing very few (variance for number of notes = 39.2). This

Table 1: Values for the seven song variables measured from three categories of song sparrow song (n = 10 birds)

Song feature	Broadcast song (N = 455)	Crystallized soft song (N = 235)	Warbled soft song (N = 207)	Friedman test	
				Q	p
No. notes	27.0 ± 1.0[a]	25.2 ± 1.0[a]	18.2 ± 2.0[b]	8.6	0.014
No. different note types	13.8 ± 0.7	13.2 ± 0.5	13.2 ± 0.9	0.6	0.741
Note variability (no. note types/no. notes)	0.54 ± 0.03[a]	0.56 ± 0.03[a]	0.81 ± 0.04[b]	12.6	0.002
Duration (ms)	2827.0 ± 69.6	2731.8 ± 84.4	2453.8 ± 168.6	4.2	0.122
Minimum frequency (Hz)	2038.7 ± 31.7[a]	1762.7 ± 41.9[b]	1539.7 ± 44.0[c]	18.2	0.000
Maximum frequency (Hz)	7992.8 ± 44.6[a]	8081.4 ± 105.2[b]	9118.0 ± 210.6[c]	15.8	0.000
Frequency range (Hz)	5965.4 ± 54.4[a]	6857.4 ± 400.5[ab]	7503.9 ± 215.9[b]	16.2	0.000

Values are given as mean ± SE.

The Friedman test assumes a chi-squared distribution with two degrees of freedom.

Shared superscripts indicate that the categories did not differ significantly according to Wilcoxon matched-pairs signed-ranks tests corrected for multiple comparisons.
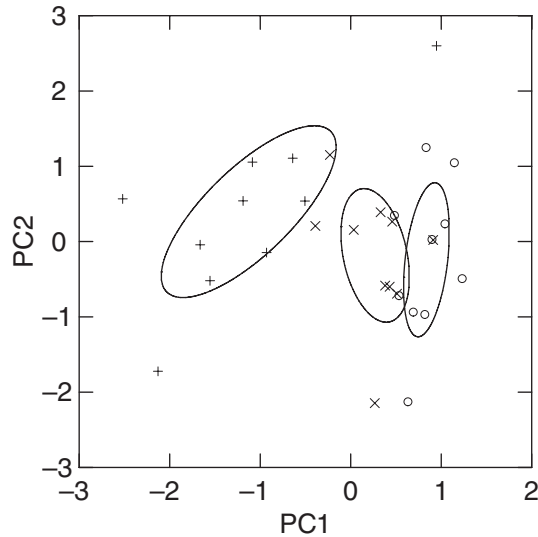
Fig. 7: Plot of PC factor scores for song characteristics of broadcast songs (○), crystallized soft songs (x) and warbled soft songs (+) generated from PCA eigenvectors. The ellipses encompass 95% confidence spaces for each of the three song categories. Points represent averaged values for each of the ten birds.

contrasts with the relatively more stereotyped number of notes comprising broadcast song and crystallized soft song (variance = 10.9 and 10.8, respectively). This difference in variances is significant (Bartlett's equality of variances test: χ^2 = 5.351; p = 0.039). Similarly, variance in song duration differs among the song categories (Bartlett's equality of variances test: χ^2 = 99.945, p < 0.001), with warbled

soft songs being much more variable in duration (variance = 618.1) compared with crystallized soft songs (variance = 294.5) and broadcast songs (variance = 190.5).

Discussion

The feature that defines soft song is, of course, its low amplitude. However, we found a continuous distribution of song amplitudes for males singing aggressively to a simulated intruder, so placement of the cutoff between loud and soft song in song sparrows is somewhat arbitrary. We tried to place our subjective cutoff at the lower limit of amplitudes produced during undisturbed, broadcast singing, but as we were able to measure amplitude rigorously only by luring the subjects to a specific perch using playback, we could not verify the cutoff with objective measurements of broadcast song amplitudes. Indeed, given that our sample of songs recorded with a measuring microphone only included songs produced in a highly aggressive context in close juxtaposition to a perceived intruder, it is possible that a more thorough sampling of songs across all contexts, including broadcast songs produced from higher song perches, might have yielded a more bimodal distribution of song amplitudes.

The broadcast song amplitudes measured here for the song sparrow are comparable with measurements of broadcast song for other species. Brackenbury (1979) measured the song amplitudes of 17
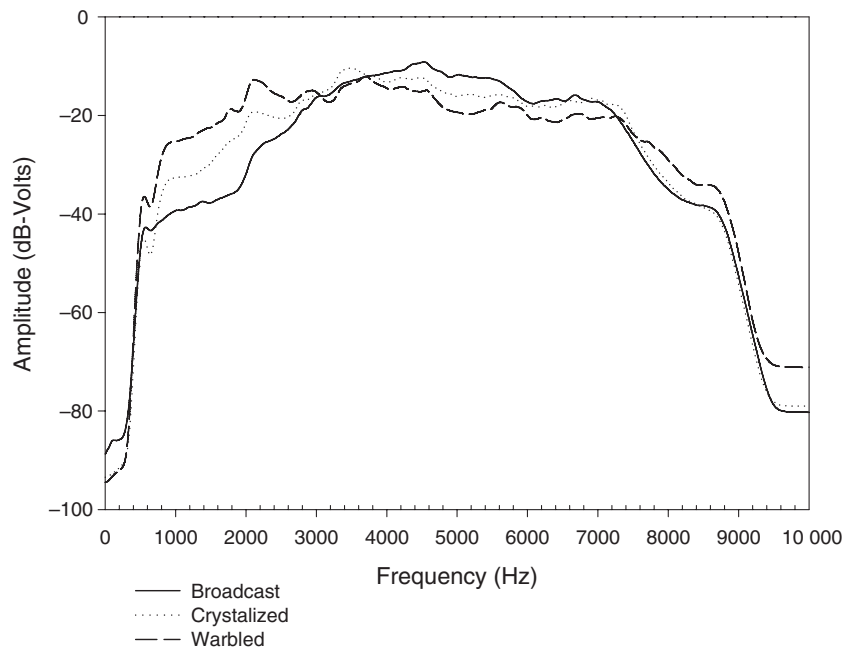

Fig. 8: Averaged power spectra for broadcast songs (n = 122), crystallized soft songs (n = 229) and warbled soft songs (n = 199) selected from playback recordings. These songs were selected for spectral analysis from the total sample because of very low levels of background noise and other extraneous sounds. Averaged spectra were created in Signal 4.0 and drawn with a 500–11,000 Hz analysis bandwidth; 1.1 Hz frequency resolution; Hanning window; 100 Hz smoothing. All songs were amplitude normalized before analysis.

British songbirds, and reported amplitudes ranging from 74 dB SPL (*Sylvia communis*) to 100 dB SPL (*Turdus philomelos*). Brenowitz (1982) reported a mean amplitude of 90.8 dB SPL (range 88.5–93.5) for the full song of a single male red-winged blackbird. Soft song amplitudes per se are unknown for other species.

Songbirds have been shown to vary song amplitudes with social context. Brumm & Todt (2004), for example, found that male nightingales (*Luscinia megarhynchos*) produce songs ranging from 66 to 73 dB SPL during solo performance and from 68 to 79 dB SPL during conspecific playback, with a significant increase in mean SPL between the former and the latter trial conditions. Similarly, Cynx & Gell (2004) reported mean amplitudes from approx. 60 to 72 dB SPL for zebra finch (*Taeniopygia guttata*) song, with higher amplitudes for birds singing in auditory and visual contact with conspecifics than for birds singing in isolation. Neither nightingales nor zebra finches produce a range of song amplitudes as broad as that produced by song sparrows, but like song sparrows they produce songs at a continuous range of amplitudes rather than in a strictly bimodal distribution of loud songs vs. soft songs.

In addition to amplitude differences, we identified a number of temporal and spectral acoustic differences between soft song and broadcast song. Based on visual assessment of spectrographic similarity, some soft songs can be categorized as low-amplitude versions of broadcast repertoire songs (crystallized soft songs), while others are categorized as non-repertoire songs that include phonology and song structure not observed in normal broadcast singing (warbled soft songs). The distinction made by subjective sorting of spectrograms between the two forms of soft song is supported by both multivariate and univariate analyses of acoustic measures. Warbled soft songs tend to include fewer notes overall than crystallized soft songs, but are also more variable, both in duration and note composition. Warbled soft songs typically lack repeated notes, or trills of repeated syllables, which are common in crystallized soft songs. Moreover, warbled soft songs contain notes at both higher and lower frequencies than crystallized soft songs, because of the inclusion of note types that are characteristic of warbled songs but less common in crystallized songs. Thus, both categorization by human observers and measurement of acoustic parameters provide evidence for two forms of soft song in the song sparrow.

One possibility raised by the significantly wider range of frequencies contained in warbled soft song

is that this class of songs might function as an honest indicator of male quality or fighting ability. Such an indicator could be an important signal during competitive assessment, and accords with the finding that the quantity of soft song produced can be used to reliably predict an attack by the singer (Searcy et al. 2006). We plan to test this hypothesis in future studies by examining how acoustic features of warbled soft song relate to male body mass, age and aggressiveness.

While soft songs in other species are sometimes considered to be broadcast songs sung quietly (reviewed in Dabelsteen et al. 1998; Morton 2000), most authors describe acoustic differences between loud and soft songs. For example, male European blackbird songs consist of full-amplitude motif elements followed by higher-pitched, quieter twitter elements (Dabelsteen 1984). When interacting with rival males, or courting females, males commonly drop the motif elements and sing 'quiet twitter songs'. Twitter songs are on average shorter in duration than full songs, and contain high-pitched warbled notes with rapid frequency modulations, resulting in higher frequency values for twitter songs (2–8 kHz) compared with motif song elements (1.5–3 kHz). In a closely related species, the redwing (*Turdus iliacus*), males produce 'broadband male aggressive twitter song' (Lampe 1991; Dabelsteen et al. 1998) consisting of high-pitched warbled notes alternated with low-pitched notes and buzzes. Titus (1998) described 'short-range songs' (low amplitude) and 'long-range songs' (full amplitude) in the dark-eyed junco (*Junco hyemalis*). Compared with long-range songs, short-range songs are longer and more complex, with more variable note sequences and fewer repetitions of syllables. Short-range songs also contain a wider range of frequencies than long-range songs, and in particular contain higher maximum frequencies. Short-range, low-amplitude songs in all three of these species thus resemble the warbled soft songs of song sparrows in acoustic features.

The only songbird other than the song sparrow that has been shown to produce more than one distinct category of soft songs is a closely related species, the swamp sparrow (*Melospiza georgiana*) (Ballentine et al. 2008). One explanation for the use of multiple categories of soft song by the birds is that the categories differ in the level of threat that they convey, but preliminary evidence does not support this hypothesis, at least not for swamp sparrows (Ballentine et al. 2008). In song sparrows, we have not yet attempted to determine whether crystallized

soft song and warbled soft song convey different levels of aggressive intent, but we have found in playback experiments that conspecific males respond with equal aggressiveness to playback of the two categories (Anderson et al. 2007). Unequal response might be expected if the two categories differed substantially in their level of threat.

An alternative to the hypothesis that crystallized soft song and warbled soft song are functionally distinct signals is that the latter category reflects vocal production error resulting from high levels of aggressive motivation. This hypothesis suggests that when distracted by a highly aggressive encounter, males may simply loosen control over song production, singing more variable, less stereotyped song. Evidence from the present study argues against this 'production error' hypothesis, however. First, warbled soft songs themselves are often composed of a particular series of notes and phrases, and can be classified as warbled song types (Fig. 4). It seems unlikely that production error would result in stereotyped songs containing the same repeated series of notes and phrases. Secondly, males sometimes alternate between normal broadcast song types and warbled soft song types, as shown in Fig. 5. Thus, males can produce normally structured song types when highly aggressive.

Another hypothesis, related to vocal production error, is that the unique acoustic features of warbled soft song may relate to the limited range of beak movements males perform when singing very softly. A consistent, positive correlation between note frequency and beak gape has been found in song sparrows (Podos et al. 1995), as well as in swamp sparrows and white-throated sparrows (*Zonotrichia albicollis*) (Westneat et al. 1993), demonstrating that beak movements influence the acoustic properties of song. In song sparrows, perhaps the unusual phonology seen in only warbled soft song occurs because these songs are sung with the beak nearly closed, and the note types that comprise broadcast songs cannot be produced in a normal tonal fashion without the full range of beak movements. This idea is consistent with our finding that the softest songs we recorded were indeed warbled soft songs.

The low transmission distance of soft song has clear implications for signal function, and several hypotheses have been proposed to explain the apparent paradox of using a low-amplitude signal to threaten rivals. One possibility is that soft song signals aggressiveness, with reliability maintained by a vulnerability handicap (Vehrencamp 2000; see also Popp 1987); the signal is only effective at close range because it will not be detected otherwise. The signaler thus places itself at risk of attack by closely approaching a rival to produce soft song, and reliability is maintained by receiver-dependent risk of attack.

Other hypotheses address the advantages of using low-amplitude signals during aggressive encounters (McGregor & Dabelsteen 1996; Dabelsteen et al. 1998; Dabelsteen 2004). Signalers engaged in an aggressive interaction may benefit from concealing the interaction from other receivers, such as territorial neighbors, mates or other females, or predators. Thus, 'eavesdropping' or 'signal interception' hypotheses explain the low-amplitude nature of soft song in terms of the benefits of concealing signaling interactions, as opposed to viewing soft song itself as having a signal function. To date, the evidence brought to bear on this idea has been negative. Searcy & Nowicki (2006) tested the benefits to territorial male song sparrows of avoiding eavesdropping by two types of third-party receivers, predators and conspecific males. If territorial males benefit from concealing signaling interactions with an intruding male from third-party males, one would predict that use of soft song by territory owners should result in fewer intrusions by third-party males. Contrary to this prediction, Searcy & Nowicki (2006) showed that intrusions by third-party males were more likely in playback trials in which the simulated owner countered an intruder's songs using soft songs than in trials in which the simulated owner countered with loud songs. In a second experiment, Searcy & Nowicki (2006) tested whether use of soft song can function to avoid predation by examining whether male song sparrows increase production of soft song in an aggressive context when they also receive alarm calls that indicate a predator is present. The proportion of soft songs produced by male song sparrows was actually significantly lower in the presence of alarm call playbacks compared with control playbacks (yellow warbler), contradicting the prediction that soft song rates should increase following conspecific predator alarm calls. The use of soft song to counter eavesdropping remains an appealing hypothesis. For example, the benefit to males of concealing signaling interactions from females has yet to be tested. However, to date there is little empirical support to suggest any benefit to signalers who sing softly during aggressive interactions.

The present study revealed that individual song sparrows sing at a remarkable range of amplitudes in an aggressive context. One explanation for this pattern is that amplitude functions as a graded

signal of aggressive motivation. Graded signals are used in aggressive signaling in a variety of taxa, and there is some evidence that vocal amplitude affects receiver response in aggressive contexts (Kroodsma 1979; Dabelsteen 1981; Gerhardt & Huber 2002; Brumm & Todt 2004). In song sparrows, Searcy et al. (2006) have shown that the number of soft songs given by a territorial male is a reliable predictor of subsequent attack on an intruder (a taxidermic mount), providing evidence that soft song signals aggressive intentions. Searcy et al. (2006) dichotomized songs as loud or soft, but as song amplitudes are continuously distributed, it may be that amplitude is actually a continuously graded signal of aggressiveness. Thus, perhaps song amplitude provides receivers with more specific information about the singer's aggressive intentions than previously realized, with amplitude inversely signaling level of aggression. This idea would be difficult to test because of the aforementioned difficulties of obtaining calibrated amplitude recordings of soft song. However, data showing that the lowest amplitude songs are given just prior to attack, or that amplitude is inversely correlated with counts of other aggressive behaviors, would support the idea of amplitude as a graded signal.

Acknowledgements

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