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Seasonal plasticity in auditory processing of the envelope and temporal fine structure of sounds in three songbirds

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ABSTRACT

Songs mediate mate attraction and territorial defence in songbirds during the breeding season. Outside of the breeding season, the avian vocal repertoire often includes calls that function in foraging, anti-predator and social behaviours. Songs and calls can differ substantially in their spectral and temporal content. Given seasonal variation in the vocal signals, the sender–receiver matching hypothesis predicts seasonal changes in auditory processing that match the physical properties of songs during the breeding season and calls outside of it. We tested this hypothesis in white-breasted nuthatches, *Sitta carolinensis*, tufted titmice, *Baeolophus bicolor*, and Carolina chickadees, *Poecile carolinensis*. We measured the envelope-following response (EFR), which quantifies phase locking to the amplitude envelope, and the frequency-following response (FFR), which quantifies phase locking to the temporal fine structure of sounds. Because songs and calls of nuthatches are amplitude modulated at different rates, we predicted seasonal changes in EFRs that match the rates of amplitude fluctuation in songs and calls. In chickadees and titmice, we predicted stronger FFRs during the spring and stronger EFRs during the winter because songs are tonal and calls include amplitude-modulated elements. In all three species, we found seasonal changes in EFRs and FFRs. EFRs varied across seasons and matched the amplitude modulations of songs and calls in nuthatches. In addition, female chickadees had stronger EFRs in the winter than in the spring. In all three species, FFRs during the spring tended to be stronger in females than in males. We also found species differences in EFRs and FFRs in both seasons; EFRs and FFRs tended to be higher in nuthatches than in chickadees and titmice. We discuss the potential mechanisms underlying seasonality in EFRs and FFRs and the implications of our results for communication during the breeding season and outside of it, when these three species form mixed-species flocks.

Reproductive cycles are mediated by changes in hormonal profiles that lead to morphological, physiological and behavioural modifications that in turn function in processes as diverse as mate attraction and production of resources for offspring (Van Tienhoven, 1983). These seasonal changes often include the production of exaggerated traits and displays to attract members of the opposite sex. During the breeding season, for instance, male songbirds produce songs that function in territory establishment and mate attraction (Catchpole & Slater, 2008). Several studies have shown how song production during the breeding season is associated with changes in testosterone levels and anatomical structures like the size of the syrinx and song nuclei in the forebrain (Brenowitz, 2004; Tramontin & Brenowitz, 2000; Tramontin, Hartman, & Brenowitz, 2000).

Congruent with seasonal changes in song production, growing evidence suggests that central and peripheral auditory processing can also change seasonally in songbirds. Some of these studies suggest that auditory processing is upregulated during the breeding season. At the level of the auditory periphery, for instance, house sparrows, *Passer domesticus*, show enhanced auditory brainstem responses to suprathreshold sounds in the frequency range of vocalizations used during the breeding season (Henry & Lucas, 2009). At higher levels of the auditory pathway, such as the caudomedial nidopallium (NCM) of the auditory forebrain, songs stimulate stronger neural responses during the breeding season in female white-throated sparrows, *Zonotrichia albicolis* (Maney, Cho, & Goode, 2006; Yoder & Vicario, 2012).

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Vocal production in songbirds, however, is not restricted to reproduction. Outside of the breeding season, the vocal repertoire of songbirds includes a variety of calls that function in group cohesion, alerting the presence of predators and announcing the presence of food (Marler, 2004). Furthermore, species that form mixed-species flocks may use heterospecific communication signals to coordinate foraging and antipredator behaviours (Goodale & Kotagama, 2008). Importantly, the physical properties of songs and calls are often very different within species. Differences in the acoustic properties of songs and calls suggest the use of different auditory specializations to process each type of vocalization. Therefore, seasonal changes in auditory processing are expected to match the physical properties of songs in the breeding season and calls outside of the breeding season. This framework of an association between signal properties and receiver processing has been described as the signal–receiver matching hypothesis (Dooling, Lohr, & Dent, 2000; Gall, Brierley, & Lucas, 2012a; Woolley, Gill, Fremouw, & Theunissen, 2009).

We asked whether seasonal plasticity in peripheral auditory processing matches seasonal changes in signal properties in white-breasted nuthatches, *Sitta carolinensis*, tufted titmice, *Baeolophus bicolor*, and Carolina chickadees, *Poecile carolinensis*, three forest species that form mixed-species flocks in the winter. Nuthatches have the simplest vocal system, followed by titmice and, with the most complex vocal repertoire, chickadees (Lucas, Freeberg, Krishnan, & Long, 2002; Fig. 1). In this manuscript, we categorize bird vocalizations by their function: we define songs as vocalizations used for reproduction purposes and we define calls as vocalizations used in other contexts (Marler & Slabbekoorn, 2004). The songs and calls of nuthatches are structurally similar and can be described as harmonic stacks that differ in duration and fundamental frequency (Ritchison, 1983). The frequency separation of the harmonics is about 500–600 Hz in nuthatch calls, and about 700–800 Hz in songs (Lucas, Vélez, & Henry, in press; Ritchison, 1983). In contrast, the physical properties of calls and songs vary tremendously in chickadees and titmice. The call repertoire in chickadees, including chick-a-dee and gargle calls, comprises a great variety of note types that include tonal and frequency-modulated elements as well as amplitude-modulated harmonic stacks (Bloomfield, Phillmore, Weisman, & Sturdy, 2005; Lucas & Freeberg, 2007; Smith, 1972). During the breeding season, male chickadees produce songs that contain four to five tonal elements with little or no frequency modulation (Lohr, Nowiki, & Weisman, 1991; Smith, 1972). Titmice songs, predominantly produced by males during the breeding season, are tonal with some slow frequency modulations (Offutt, 1965). During the winter, titmice also produce chick-a-dee calls with elements that can be tonal, frequency-modulated or amplitude-modulated harmonic stacks (Offutt, 1965; Owens & Freeberg, 2007). A property of harmonic sounds, like nuthatch vocalizations and some elements of the calls of chickadees and titmice, is that the separation between frequency elements generates amplitude modulations in the sound envelope at the rate of the frequency separation (Moore, 1993; Viemeister & Plack, 1993). Importantly, the auditory system can process these amplitude fluctuations (Henry, 1997; Lucas et al., in press; Simmons & Buxbaum, 1996), which underscores the importance of different dimensions of acoustic signals for communication (Nelson & Marler, 1990).

We used auditory evoked potentials (AEPs) to evaluate how the auditory system of nuthatches, titmice and chickadees processes tonal and amplitude-modulated sounds during the breeding (spring) and nonbreeding (winter) seasons. AEPs are voltage

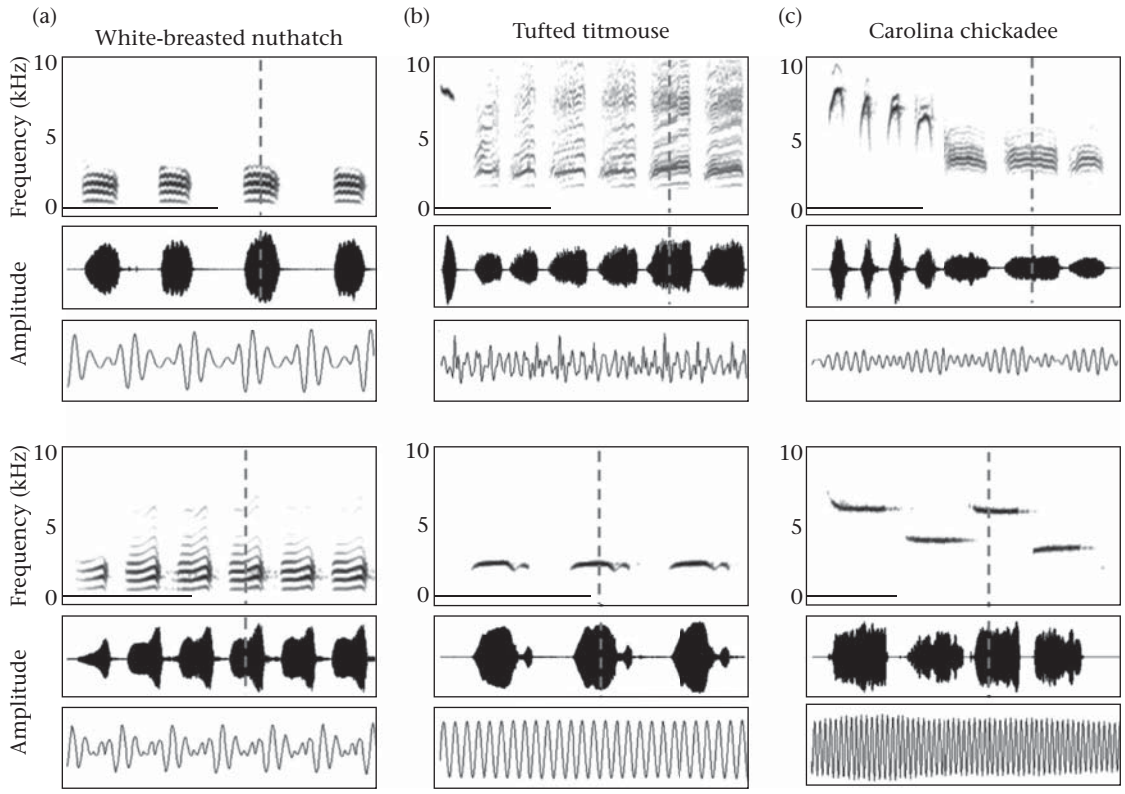

Figure 1. Calls (top row) and songs (bottom row) of (a) white-breasted nuthatches, (b) tufted titmice and (c) Carolina chickadees. The top panel is the spectrogram and the middle panel is the oscillogram of each vocalization. Scale bar in each spectrogram represents 0.5 s. The bottom panel depicts 10 ms of the oscillogram through the dashed vertical grey line in the spectrogram and in the oscillogram of the entire vocalization. Oscillograms are plotted as the normalized amplitude (between +1 and −1) as a function of time.

changes that result from hair cell (i.e. cochlear) or neural (i.e. auditory nerve, brainstem and possibly midbrain) activity caused by acoustic input and are measured with surface electrodes on the scalp (Hall, 2007). We measured the envelope-following response (EFR) and the frequency-following response (FFR). The EFR is a measurement of the auditory system's ability to phase-lock to the rate of modulation in the amplitude envelope of a sound (Boston & Møller, 1985; Hall, 2007) and has been used to investigate temporal processing across a number of different taxa (Basu, Krishnan, & Weber-Fox, 2010; Burton, Cohen, Rickards, McNally, & Clark, 1992; Dolphin & Mountain, 1992; Finneran, London, & Houser, 2007; Henry & Lucas, 2008; Henry, Gall, Bidelman, & Lucas, 2011; Parthasarathy & Bartlett, 2012). The FFR represents the ability of the auditory system to phase-lock to the temporal fine structure of sounds and has been widely used to investigate speech processing in humans (Boston & Møller, 1985; Chandrasekaran & Kraus, 2010; Hall, 2007). Authors have also started to explore FFR properties in nonhuman animals (Du, Ma, Wang, Wu, & Li, 2009; Parthasarathy & Bartlett, 2012; Popov & Supin, 1988). In fact, Lucas, Freeberg, Long, and Krishnan (2007) investigated seasonal patterns in FFRs in songbirds. Here, we investigate seasonal plasticity in two complementary properties of the auditory system: auditory processing of the amplitude envelope and the temporal fine structure of sounds.

Based on the hypothesis that seasonal changes in auditory processing should match song and call properties, we predicted stronger FFRs during the spring and stronger EFRs in winter in chickadees and titmice because songs are tonal and calls include strong amplitude modulations. Given the differences in the rate of amplitude modulations in nuthatch songs and calls, we predicted that nuthatches would have stronger EFRs to the 700 Hz rates of fluctuation in song in the spring compared to the winter. When comparing across species in the spring, we predicted stronger EFRs in nuthatches than in chickadees and titmice, and stronger FFRs in chickadees and titmice than in nuthatches because nuthatch songs are amplitude modulated and titmice and chickadee songs are tonal. In the winter, we predicted strong and similar EFRs in all species, and stronger FFRs in chickadees and titmice since some of the call elements of these species are tonal.

GENERAL METHODS

Subjects and Study Sites

The protocols for collecting, handling and testing animals were approved by the Purdue Animal Care and Use Committee (PACUC no. 1111000125). We conducted this study between January 2012 and December 2013. Birds were collected in the morning with mist nets or treadle traps baited with mixed seed at the Ross Biological Reserve (40°24′30″N, 87°04′30″W), Martell Forest (40°25′58″N, 87°02′ 20″W), the Purdue Wildlife Area (40°26′30″N, 87°03′30″W) and at one private residence in West Lafayette, IN, U.S.A. Birds were brought to an indoor aviary at Purdue University where they were housed individually in 1 m^3 stainless-steel mesh cages and provided with ad libitum water, sunflower seed, mealworms and grit. For this study, we divided the testing of birds into two seasons: 'winter', ranging from October to January, and 'spring', from February to June. We chose February as the beginning of the spring because social flocks start breaking up into male–female pairs and reproductive hormones and song rates begin to increase around that time in our study population (Ball, 1999; Lucas, Freeberg, Egbert, & Schwabl, 2006; Smith, 1991). We tested only adults; juvenile status was determined using outer retrix shape in titmice and chickadees, and mouth colour in titmice and nuthatches (Pyle, 1997). In the winter, we tested 10 white-breasted nuthatches (4 females, 6 males), 10 titmice (6 females, 4 males) and 12 Carolina chickadees (7 females, 5 males). During the spring, we tested 12 nuthatches (4 females, 8 males), 20 titmice (12 females, 8 males) and 15 chickadees (3 females, 12 males). Sex was determined using plumage patterns in nuthatches and wing chord in titmice (males: ≥80 mm; females: <80 mm) and chickadees (males: ≥62 mm; females: <62 mm). Wing chord thresholds to determine sex in our study population have been validated through the presence of brood patches (Thirakhupt, 1985), laparotomy (Lucas, Peterson, & Boudinier, 1993) and dissections (Lucas et al., 2006). Average ± SD body mass right before acquiring their AEPs was 20.1 ± 0.8 in nuthatch females, 20.8 ± 1.1 g in nuthatch males, 20.4 ± 0.9 g in titmice females, 22.8 ± 1.6 g in titmice males, 9.5 ± 0.3 g in chickadee females and 10.5 ± 0.5 g in chickadee males. We fitted each bird with a uniquely numbered aluminium leg band or coloured leg rings. Typically, we conducted auditory tests on the afternoon of the day of capture and we released the subjects at their capture location within 2 days after testing. Subjects were released only after they were feeding, flying and vocalizing normally in the cages. When released, the birds readily flew from perch to perch and vocalized; these are all signs that the birds are in good physical condition.

Auditory Test Equipment and Procedure

All auditory experiments were conducted inside an anechoic sound chamber (1.2 × 1.2 × 1.4 m) lined with 7.2 cm Sonex foam (Acoustics Solutions, Richmond, VA, U.S.A.). Prior to testing, subjects were weighed and anaesthetized with an injection into the breast muscle of midazolam (4.5–5.5 mg/kg), ketamine (45–55 mg/kg) and xylazine (45–55 mg/kg). If necessary, subjects were given a supplemental injection with half the dose about 50 min into testing in order to complete the entire set of auditory tests (in approximately 75 min). We then positioned the subjects at the centre of the chamber on a pre-warmed heating pad (Snuggle-Safe pad at 52 °C) covered with several layers of towel. The temperature between the subject's body and the outermost towel layer was monitored with a thermistor and maintained at 39 ± 1.5 °C by adding or removing layers of towel.

We used a Tucker Davis Technologies III mounted-rack system (TDT, Alachua, FL, U.S.A.) and a Dell PC running BioSig32 software in a room adjacent to the sound chamber to coordinate stimulus presentation and response acquisition. Digital stimuli were generated in SigGenRP with a sampling rate of 20 kHz, converted to analogue signals with a TDT RP2 real-time processor, equalized across frequencies with a 31-band equalizer (Ultragraph Pro FBQ 6200), amplified with a TDT SA1 amplifier, and presented through an electromagnetically shielded overhead speaker (JBL Control 25 AV; 80–16 000 Hz frequency response) suspended 50 cm above the subject. Sound levels were calibrated within ±2 dB SPL (sound pressure level; re. 20 μPa) with Larson Davis Sound Track LxT1 sound level meter and a 377B02 microphone at the approximate position of a subject's ear.

AEPs were recorded through subdermal needle electrodes (Nicolet Biomedical, Fitchburg, WI, U.S.A.) placed under the skin at the crown of the head (positive electrode), the mastoid just posterior to the right ear (negative electrode) and the nape of the neck (common ground). We measured interelectrode impedance to check the integrity and placement of the electrodes and proceeded with testing only when impedance was less than 7 kΩ. The electrodes fed into a TDT RA4LI headstage and responses were amplified (200 k) and digitized (24.41 kHz) with a TDT RA4PA Medusa bioamplifier. Responses were then resampled (48.82 kHz), bandpass filtered between 0.1 and 5 kHz, notch filtered at 60 Hz with a TDT RA16 Medusa Base Station and stored in the computer.

Auditory tests described below began and ended by running a standard click at 80 dB SPL. The stereotypical response to click standards (Lucas et al., 2002) lets us use click-evoked potentials to identify birds with abnormal auditory systems and as an additional check for electrode placement. In addition, click standards were used to ensure the bird's auditory system did not change over the course of the test.

Envelope-following Response

EFR stimuli were sinusoidally amplitude-modulated (SAM) tones generated using the following equation:

$$A \times [1 + m \times \sin(2\pi \times fm \times t)] \times \sin(2\pi \times fc \times t + \rho)$$

where A is a scaling factor, m is the modulation index (1.0 in all cases), fm is the rate of amplitude modulation (AM rate) in hertz (200, 300, 400, 500, 700 or 900), fc is the frequency of the carrier in hertz (3000 in all cases), ρ is the starting phase of the carrier (90° or 270°) and t is time in seconds. SAM tones were 53.3 ms long, shaped with 3 ms $\cos^2$ onset/offset ramps, broadcast at 72 dB SPL and presented at a rate of 13.1 stimuli/s. We obtained two replicates for each modulation frequency, each one averaged over 300 presentations of the stimulus and with a carrier starting phase of either 90° or 270°.

EFRs were sampled during a 65 ms window that started with the stimulus onset. We exported the average AEP of each replicate for each modulation frequency as a text file and analysed them with custom-made codes in PRAAT (version 4.6; Boersma, 2001). The auditory system can phase-lock to the amplitude fluctuations of the stimulus (Henry, 1997; Simmons & Buxbaum, 1996). Therefore, we generated a frequency spectrum of each AEP with a fast Fourier transform (sampling rate = 48.82 kHz; FFT size = 4096 points; frequency resolution 11.92 Hz) and estimated the EFR as the amplitude of the spectrum (in dBnV) at the modulation frequency of the stimulus. We then measured the noise floor by averaging the amplitude of the spectrum two frequency bins above and below the modulation frequency. We only included in the analysis EFR amplitudes that were higher than 3 dB above this noise floor.

Frequency-following Response

Stimuli used to obtain FFRs were 20 ms tones gated with 3 ms onset/offset ramps. We tested four stimulus frequencies: 0.5, 1, 2 and 3 kHz. For each test frequency, we recorded two replicates of 300 presentations each, one with a starting phase of 90° and the other with a starting phase of 270°. Tones were broadcast at 72 dB SPL with a rate of 24.3 stimuli/s. We chose 72 dB stimuli because previous studies have shown that AEPs to clicks and tones at this level are robust and not overly contaminated by cochlear microphonic signal (Lucas et al., 2002, 2007). However, we also measured FFRs to the same tones broadcast at 80 dB SPL and 64 dB SPL and found the same pattern of results reported below for 72 dB stimuli (see Supplementary Material). Similarly, we measured FFRs in response to 4 kHz tones for a subset of subjects of each species. FFRs to 4 kHz tones were often weak and less than 3 dB above the noise floor. For this reason, we did not include frequencies above 3 kHz in our analysis.

Auditory evoked responses were acquired during a 30 ms window starting at the onset of the stimulus. We exported the average AEP waveform for both replicates at each frequency as text files and analysed them with custom-made codes in PRAAT (version 4.6; Boersma, 2001). We calculated the frequency spectrum of the AEP (sampling rate = 48.82 kHz; FFT size = 2048 points; frequency resolution 23.84 Hz) and measured the amplitude of the spectrum (in dBnV) at the frequency of the stimulus. For the FFR analysis, we also measured the noise floor by averaging the amplitude of the spectrum two frequency bins above and below the stimulus frequency and included in the analysis FFR amplitudes that were higher than 3 dB above the noise floor.

Statistical Analyses

We analysed AEPs using repeated measures (rm) ANOVAs with Proc MIXED in SAS v.9.2. We specified the Kenward–Roger method to calculate degrees of freedom and a first-order autoregressive covariance structure for all models. We used the command 'LSMEANS' within Proc MIXED to estimate least square means (LS means) and post hoc tests for pairwise comparisons (LSMEANS/diff). LS means are useful to describe patterns associated with a specific variable holding other factors constant. We confirmed that the assumptions of normality of residuals and homogeneity of variance were met using Proc UNIVARIATE.

We analysed our data in two ways. First, we tested species differences for each season separately. In these analyses, we included species, sex and either AM rate (EFRs) or frequency (FFRs) as independent variables and either EFR or FFR strength as the dependent variable. Second, we tested for seasonal changes in auditory processing within each species. For such analyses, we included season, sex and either AM rate (EFRs) or frequency (FFRs) of the signal as independent variables and either EFR or FFR strength as the dependent variable. We included all main effects and interaction terms in the models.

RESULTS

Envelope-following Response

All species by season

In Fig. 2, we show the modulation rate transfer function (MRTF) of each species in the winter (Fig. 2a) and the spring (Fig. 2b). MRTFs plot the strength of the EFR as a function of amplitude modulation rate (AM rate). We found a significant species∗AM rate interaction (Table 1) in the winter (Fig. 2a). EFR amplitude was significantly lower in chickadees than in titmice ($t_{145} = 2.9$, $P = 0.004$) and nuthatches ($t_{144} = 3.7$, $P = 0.0003$) when the AM rate was 500 Hz. We also found a significant main effect of AM rate (Table 1); EFR amplitudes were highest at 400 and 500 Hz, and decreased at lower and higher AM rates. We found no significant main effects of species or sex, nor significant species∗sex, sex∗AM rate, or species∗sex∗AM rate interactions (Table 1).

The analysis of EFR amplitude in the spring revealed a significant species∗sex∗AM rate interaction (Table 1). This three-way interaction led to significant AM rate∗sex and species∗AM rate (Fig. 2b) interactions, and a marginally significant species∗sex interaction (Table 1). The rmANOVA also revealed significant main effects of species and AM rate (Table 1). Averaged across the entire data set, EFR amplitudes were highest at 300 and 400 Hz, and decreased at lower and higher AM rates. The strength of the EFR was lower in chickadees than in titmice and nuthatches (both $t_{78.6–79.1} > 3.7$, $P < 0.0005$). We further explored the three-way and two-way interactions with species-specific rmANOVAs including season, sex and AM rate as independent variables.

Each species across seasons

In nuthatches, we found a significant season∗frequency interaction (Table 2, Fig. 3a). In the winter, EFR amplitude showed a relatively sharp peak at a modulation frequency of 500 Hz. In the spring, EFR amplitudes showed a broad peak from 300 Hz to 700 Hz. Compared to the winter, EFR amplitude was significantly

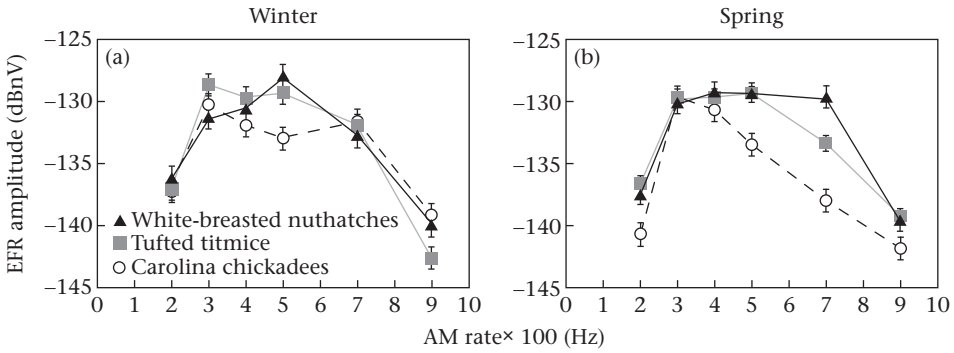

Figure 2. Modulation rate transfer functions plotting envelope-following response (EFR) amplitude as a function of amplitude modulation rate for each species in the (a) winter and (b) spring. Symbols represent LSmeans ± SE for nuthatches, titmice and chickadees.

Table 1
Repeated measures ANOVAs for envelope-following response (EFR) amplitude measured during the winter and the spring

Effect	Winter			Spring		
	F	*df*	Pr>*F*	*F*	*df*	Pr>*F*
Species	0.39	2, 49.8	0.6773	9.04	2, 79.9	**0.0003**
Sex	0.01	1, 49.8	0.9827	1.38	1, 79.7	0.2433
Species∗sex	1.1	2, 49.8	0.3407	3.09	2, 79.9	0.0509
AM rate	71.89	5, 355	**<0.0001**	100.26	5, 505	**<0.0001**
Species∗AM rate	4.32	10, 358	**<0.0001**	6.51	10, 509	**<0.0001**
AM rate∗sex	1.7	5, 355	0.1344	3.14	5, 505	**0.0084**
Species∗AM rate∗sex	0.7	10, 358	0.7201	3.56	10, 509	**0.0001**

AM: amplitude modulation. Significant results are shown in bold.

higher at a modulation frequency of 700 Hz in the spring ($t_{141} = 2.52$, $P = 0.013$).

In titmice, we found a significant season∗AM rate interaction (Table 2, Fig. 3b); EFR amplitudes were lower at 900 Hz in the winter than in the spring ($t_{213} = 3.39$, $P = 0.0008$). We also found a significant sex∗AM rate interaction in titmice (Table 2, Fig. 4): males had higher EFR amplitudes than females at 200 Hz ($t_{178} = 4.46$, $P < 0.0001$) and 900 Hz ($t_{171} = 2.11$, $P = 0.036$). This interaction resulted in a significant main effect of sex (Table 2), with males having higher EFR amplitudes than females.

In chickadees, we found a significant season∗frequency interaction (Table 2, Fig. 3c) with a 6 dB difference in EFR amplitude between the spring and the winter at 700 Hz ($t_{138} = 4.30$, $P < 0.001$) and a 3 dB difference at 200 Hz ($t_{143} = 2.21$, $P = 0.021$). This interaction was due to a significant season∗sex∗frequency interaction (Table 2). In female chickadees, EFR amplitude was about 10 dB lower at 700 Hz in the spring than in the winter

Table 2
Repeated measures ANOVAs for envelope-following response (EFR) amplitude measured for white-breasted nuthatches (WBNU), tufted titmice (ETTI) and Carolina chickadees (CACH)

Effect	WBNU			ETTI			CACH		
	F	*df*	Pr>*F*	*F*	*df*	Pr>*F*	*F*	*df*	Pr>*F*
Season	0.22	1, 42.6	0.6392	0.03	1, 66.7	0.8621	2.91	1, 46.9	0.0945
Sex	2.52	1, 29.7	0.1232	7.13	1, 55.6	**0.0099**	0.38	1, 40.6	0.5436
Sex∗season	0.03	1, 42.6	0.8611	0.6	1, 67.7	0.4409	0.21	1, 46.9	0.6481
AM rate	56.43	5, 235	**<0.0001**	100.26	5, 346	**<0.0001**	39.91	5, 276	**<0.0001**
Season∗AM rate	2.57	5, 235	**0.0274**	3.58	5, 346	**0.0036**	7.34	5, 276	**<0.0001**
Sex∗AM rate	1.15	5, 235	0.3342	3.2	5, 346	**0.0077**	1.17	5, 276	0.3237
Sex∗season∗AM rate	0.93	5, 235	0.464	2.03	5, 346	0.0733	3.87	5, 276	**0.0021**

AM: amplitude modulation. Significant results are shown in bold.

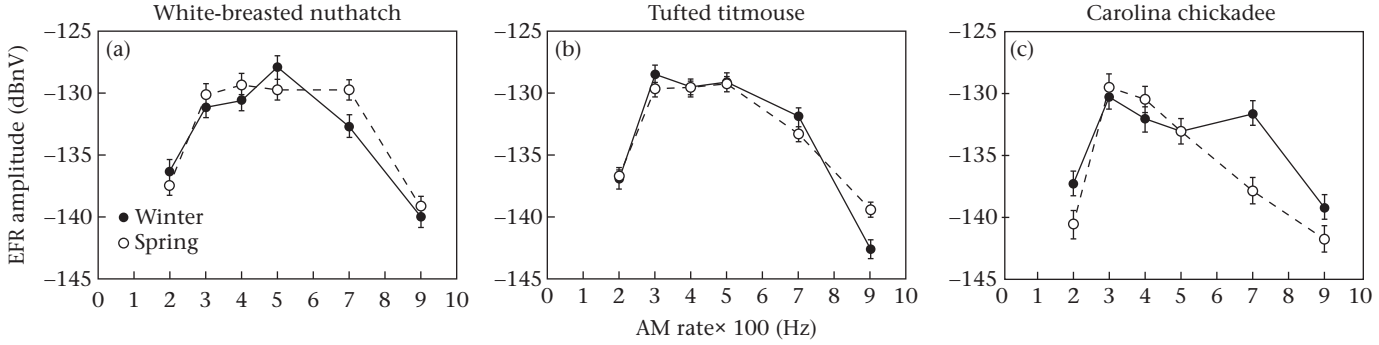

Figure 3. LSmean ± SE envelope-following response (EFR) amplitude as a function of amplitude modulation rate in the winter and spring for (a) nuthatches, (b) titmice and (c) chickadees.

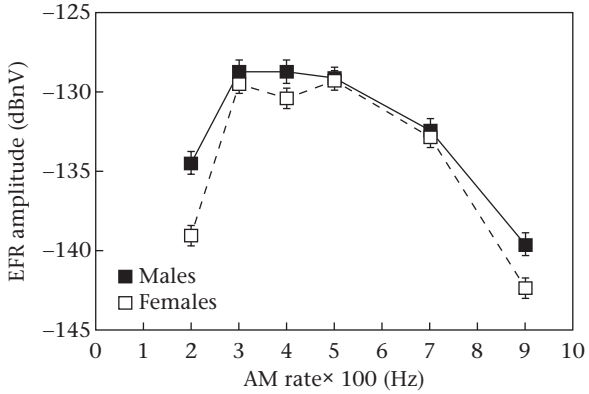

Figure 4. LSmean ± SE envelope-following response (EFR) amplitude as a function of modulation rate in titmice males and females.

($t_{144} = 4.33$, $P < 0.0001$; Fig. 5a). In male chickadees, EFR amplitude was about 6 dB lower at 200 Hz in the spring than in the winter ($t_{127} = 3.14$, $P = 0.002$; Fig. 5b).

Frequency-following Response

All species by season

In the winter, we found a significant main effect of species (Table 3, Fig. 6a): overall FFR amplitudes were higher in nuthatches than in chickadees ($t_{34.7} = 2.23$, $P = 0.033$) and titmice ($t_{35.34} = 3.63$, $P = 0.0009$). There was also a significant main effect of frequency (Table 3). FFR amplitude was highest at 0.5 kHz (all $t_{218–235} > 6.5$, $P < 0.0001$) and lowest at 3 kHz (all $t_{218–235} > 2.2$, $P < 0.002$). We found no significant main effect of sex, nor significant species∗sex, species∗frequency, frequency∗sex or species∗sex∗frequency interactions (Table 3).

In the spring, the analyses of FFR amplitude revealed a significant sex∗frequency interaction ($F_{3,285} = 4.03$, $P = 0.008$) and a significant main effect of frequency (Table 3). We found a marginally significant species∗sex∗frequency interaction and a nonsignificant species∗frequency interaction (Table 3, Fig. 6b); these interactions, however, were significant when the stimuli were played back at 64 and 80 dB SPL (see Supplementary Table S1). We further explored these patterns with species-specific mANOVAs in which we included season, sex and frequency as independent variables.

Each species across seasons

Within species, FFR amplitude to each particular stimulus was similar across seasons (Table 4, Fig. 7).

Table 3
Repeated measures ANOVAs for frequency-following response (FFR) amplitude measured during the winter and the spring

Effect	Winter			Spring		
	F	*df*	Pr>*F*	*F*	*df*	Pr>*F*
Species	6.66	2, 35.3	**0.0035**	2.31	2, 39.8	0.1129
Sex	0.06	1, 35.3	0.8048	1.65	1, 39.5	0.2059
Species∗sex	0.78	2, 35.3	0.4644	0.37	2, 39.8	0.696
Frequency	52.02	3, 215	**<0.0001**	54.23	3, 285	**<0.0001**
Species∗frequency	0.66	6, 218	0.6806	1.49	6, 286	0.1812
Frequency∗sex	1.18	3, 215	0.3199	4.03	3, 285	**0.0079**
Species∗frequency∗sex	1.59	6, 218	0.1506	1.96	6, 286	0.072

Significant results are shown in bold.

In nuthatches, we found a significant main effect of frequency (Table 4), with the highest FFR amplitudes at 500 Hz (all $t_{129–142} > 5.4$, $P < 0.0001$) and the lowest at 3 kHz (all $t_{131–142} > 2.3$, $P < 0.025$). We also found a marginally significant season∗sex∗frequency interaction (Table 4); this interaction reached significance when stimuli were broadcast at 80 dB SPL (see Supplementary Table S2). In general, FFR amplitudes varied little between males and females in the winter, but were higher in females than in males in the spring, particularly at 1 kHz (see Supplementary Fig. S2). We found no significant main effects of sex or season, nor significant season∗sex, season∗frequency or sex∗frequency interactions (Table 4).

In titmice, we found a significant main effect of frequency (Table 4), with the highest FFR amplitudes at 500 Hz (all $t > 9.5$, $P < 0.0001$) and the lowest at 3 kHz (all $t > 5.24$, $P < 0.0001$). We also found a significant season∗sex interaction (Table 4): in females, FFR amplitude was about 3.5 dB higher in the spring compared to the winter ($t_{58.1} = 2.04$, $P = 0.046$). We found no significant main effects of season or sex, nor significant, season∗frequency, sex∗frequency or season∗sex∗frequency interactions (Table 4).

In chickadees, we found a significant main effect of frequency (Table 4), with FFR amplitudes higher at 500 Hz than at all other frequencies (all $t_{163–192} > 7.14$, $P < 0.0001$) and higher at 1 kHz than at 2 kHz ($t_{164} = 2.97$, $P = 0.003$) and 3 kHz ($t_{188} = 3.02$, $P = 0.003$). The rmANOVA also revealed a significant season∗sex∗frequency interaction (Table 4), which was also significant when the tones were broadcast at 64 dB SPL (see Supplementary Table S2). In general, female chickadees showed stronger FFRs than males in the spring, particularly at 3 kHz (Fig. 8, Supplementary Fig. S5). We found no significant main effects of sex or season, nor significant season∗sex, season∗frequency or sex∗frequency interactions (Table 4).

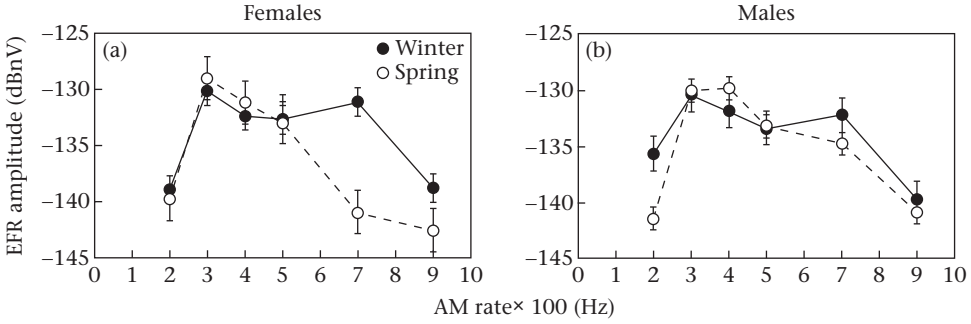

Figure 5. Modulation rate transfer functions for chickadee (a) females and (b) males obtained in the winter and spring.

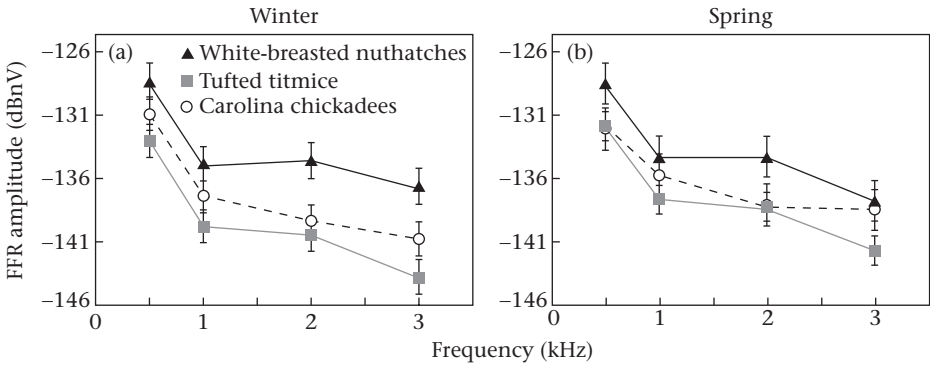

Figure 6. LSmean ± SE frequency-following response (FFR) amplitude as a function of stimulus frequency in the (a) winter and (b) spring for nuthatches, titmice and chickadees.

Table 4
Repeated measures ANOVAs for frequency-following response (FFR) amplitude measured for white-breasted nuthatches (WBNU), tufted titmice (ETTI) and Carolina chickadees (CACH)

Effect	WBNU			ETTI			CACH		
	F	*df*	Pr>*F*	*F*	*df*	Pr>*F*	*F*	*df*	Pr>*F*
Sex	1.14	1, 17.6	0.299	0.21	1, 30	0.653	0.82	1, 22.6	0.3757
Season	0.23	1, 26.9	0.6364	0.35	1, 68	0.5544	1.65	1, 33.2	0.2084
Sex∗season	0.78	1, 26.9	0.3849	4.09	1, 68	**0.047**	0.19	1, 33.2	0.06624
Frequency	22.7	3, 131	**<0.0001**	62.89	3, 202	**<0.0001**	32.1	3, 174	**<0.0001**
Sex∗frequency	1.27	3, 131	0.2872	1.71	3, 202	0.1663	1.05	3, 174	0.3734
Season∗frequency	0.21	3, 132	0.8899	0.33	3, 201	0.8052	1.71	3, 173	0.1659
Sex∗season∗frequency	2.52	3, 132	0.061	2.14	3, 201	0.0968	3.97	3, 173	**0.0091**

Significant results are shown in bold.

DISCUSSION

Seasonal changes in auditory processing, and the importance of hormones mediating these changes, have been demonstrated in fish (Sisneros, Forlano, Deitcher, & Bass, 2004), frogs (Goense & Feng, 2005; Hillery, 1984), birds (Caras, Brenowitz, & Rubel, 2010; Maney et al., 2006; Yoder & Vicario, 2012) and mammals (Hultcrantz, Simonoska, & Stenberg, 2006). In general, these studies show upregulation of hearing properties like higher auditory sensitivity to tone bursts (Goense & Feng, 2005; Hillery, 1984), enhanced spectral resolution (Gall, Salameh, & Lucas, 2013) or stronger overall responses to sexual acoustic communication signals (Maney et al., 2006; Yoder & Vicario, 2012). Importantly, acoustic communication signals are multidimensional (Nelson & Marler, 1990), and the processing of each dimension cannot be fully explained by single properties of the auditory system. Our study adds to this line of research by showing seasonal plasticity in two complementary properties of the auditory system. We show that species differ in the extent to which season and sex affect auditory processing of the envelope (EFR) and the temporal fine structure (FFR) of sounds. Consistent with the sender–receiver matching hypothesis, seasonal changes in auditory processing in nuthatches and chickadees match the acoustic properties of songs during the breeding season and of calls outside of the breeding season. We also report species differences in EFRs and FFRs within seasons. We now discuss how these results relate to previous work and the implications of our results for communication during and outside of the breeding season.

Auditory Processing of the Amplitude Envelope of Sounds (EFRs)

We found species differences in the MRTF both in the spring and the winter. While the difference was stronger in the spring, nuthatches tended to have stronger EFRs than chickadees and titmice in both seasons. Strong EFR amplitudes in nuthatches are consistent with our predictions based on song and call properties because

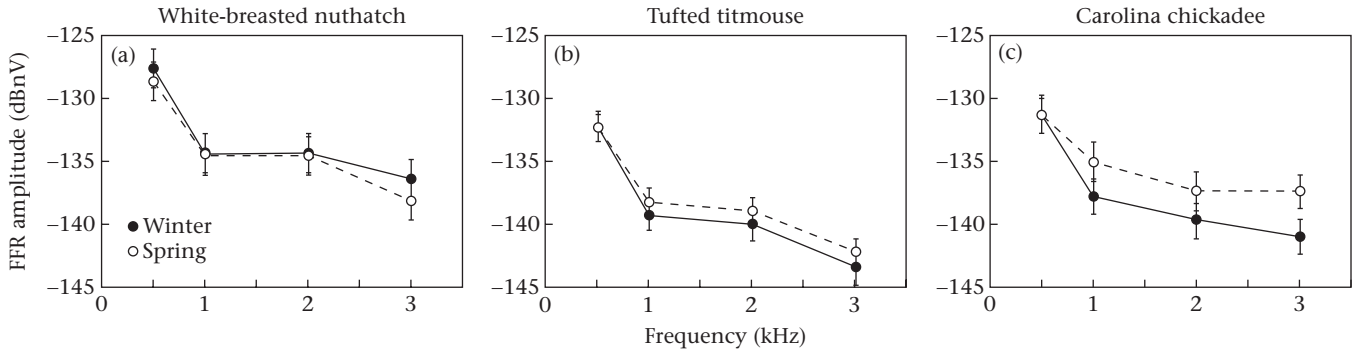

Figure 7. LSmean ± SE frequency-following response (FFR) amplitude as a function of stimulus frequency in the winter and spring for (a) nuthatches, (b) titmice and (c) chickadees.

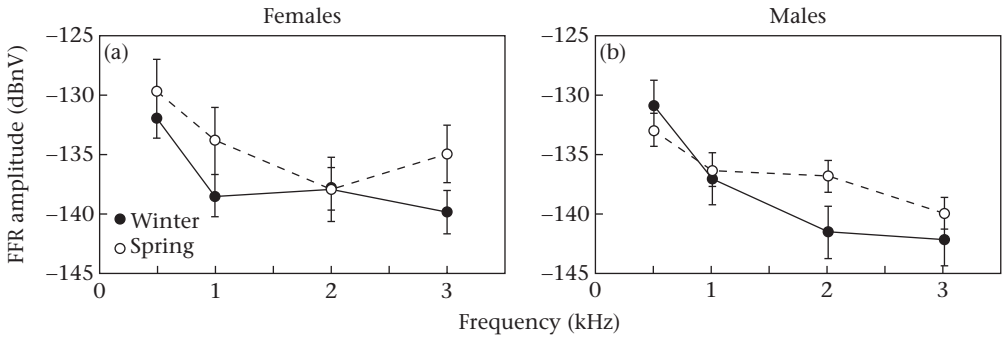

Figure 8. LSmean ± SE frequency-following response (FFR) amplitude as a function of stimulus frequency for chickadee (a) females and (b) males obtained in the winter and spring.

the harmonic structure of nuthatch songs and calls generate strong amplitude modulations in the sound envelope.

An interesting seasonal change in auditory processing is the broadening of the MRTF in nuthatches during the breeding season. In the winter, the MRTF of nuthatches peaks at 500 Hz and decreases at higher and lower frequencies. In the spring, the MRTF extends up to 700 Hz. This change matches the properties of nuthatch calls and songs (Fig. 1). The frequency separation of the harmonics in the nuthatch call generates amplitude modulations close to 500 Hz, while the frequency separation in the song generates amplitude modulations close to 700 Hz (Lucas et al., in press; Ritchison, 1983). Therefore, the broadening of the MRTF during the breeding season may be an adaptation to better process the amplitude modulations inherent to the harmonic structure of the song. It is important to note that we did not find sex differences in EFRs, suggesting that males and females process the envelope of songs and calls similarly.

We also discovered a narrowing of the MRTF in female chickadees during the breeding season. This seasonal change in MRTF shape may also be an adaptation for enhanced processing of song properties during the breeding season. Chickadee songs are tonal and the change in frequency from one element to another is an important feature indicating male quality in black-capped chickadees, *Poecile atricapillus* (Christie, Mennill, & Ratcliffe, 2004). This suggests that females may benefit from an auditory system with acute spectral resolution. In fact, females have been shown to have better spectral resolution than males in Carolina chickadees (Henry & Lucas, 2010) and brown-headed cowbirds, *Molothrus ater* (Gall & Lucas, 2010).

The narrowing of the MRTF during the breeding season could be a result of an enhancement of spectral resolution in female chickadees. The auditory system of birds and mammals is usually described as a bank of band-pass auditory filters (Moore, 1993). The auditory filter bank acts in ways similar to a Fourier analysis and decomposes broadband sounds into different frequency components (Bradbury & Vehrencamp, 1998; Fletcher, 1940). Auditory filters vary in bandwidth, and narrower filters provide greater spectral resolution because sounds of similar frequencies are more likely to be processed by different channels (Moore, 1993). However, high spectral resolution comes at the expense of low temporal resolution. Narrow auditory filters integrate signals over relatively longer periods, which hinders the ability of the auditory system to follow rapid changes in amplitude over time. Therefore, narrow auditory filters have poor temporal resolution compared to broad auditory filters. Lower EFR amplitudes at higher amplitude modulation frequencies is evidence for decreased temporal resolution because the auditory system is less able to follow fast changes in amplitude over time (Dolphin, Au, Nachtigall, & Pawloski, 1995; Gall, Henry, & Lucas, 2012b; Henry & Lucas, 2008). Hence, seasonal changes in EFRs in female chickadees may be due to seasonal changes in auditory filter bandwidth (i.e. narrow filters in the spring and wide filters in the winter). In fact, Gall et al. (2013) recently reported seasonal changes in auditory filter bandwidth in female house sparrows, but not in male house sparrows. Compared to the nonbreeding season, female house sparrows had narrower auditory filters during the breeding season, which led to a reduction in temporal resolution (Gall et al., 2013). These results suggest that spectral acuity may be more important than temporal acuity for mate selection during the breeding season in both female chickadees and female house sparrows.

In titmice, EFR amplitude at 900 Hz was stronger in the spring than in the winter. The biological significance of this spring increase in processing of fast amplitude modulations is intriguing for two reasons. First, titmice songs are not amplitude modulated and therefore there is no expectation of better processing of amplitude-modulated sounds during the breeding season. Second, fast amplitude modulation rates (up to 1.4 kHz) are present in titmice calls (Henry & Lucas, 2008), which suggest that processing of fast amplitude modulations should be better in the winter when calls are more commonly produced than songs. Regarding sex differences in titmice, MRTFs are also consistent with narrower auditory filters in females than in males. These results suggest that sexual selection for enhanced spectral resolution may have a stronger effect on females. This effect, however, was weaker in titmice than in chickadees. Our results suggest that it will be important to measure seasonal patterns in auditory filter bandwidth in these species.

Auditory Processing of the Temporal Fine Structure of Sounds (FFRs)

We predicted higher FFR amplitudes in chickadees and titmice than in nuthatches because their vocalizations include tonal elements while nuthatch vocalizations have strong amplitude modulations. However, FFR amplitudes tended to be higher in nuthatches and lower in titmice. The strong FFR amplitudes in nuthatches suggest that processing of the spectral content of songs and calls may be of great importance for communication purposes (Lucas et al., in press). Compared to chickadees, the weak FFRs in titmice have been previously interpreted as the result of sexual selection acting on a simpler vocal communication system (Lucas et al., 2007).

Our results show upregulation of FFRs during the breeding season in female chickadees and titmice. In nuthatches, females also tended to have higher FFRs during the spring, but the pattern more likely represents a downregulation of FFR in males. While weaker at some signal levels, these patterns were consistent between 64 dB and 80 dB SPL (see Supplementary Figs. S2–S5). These results parallel, to a great extent, those reported previously. Lucas

et al. (2007) showed little variation in FFR amplitude across seasons in titmice, an increase in FFRs during the spring in chickadees and an increase in the winter in nuthatches. Together, these results suggest that processing of the temporal fine structure of songs during the breeding season may be relatively more important to females than it is to males in each of these three species.

Underlying Mechanisms of Seasonal Patterns in EFRs and FFRs

The generators of EFRs and FFRs in birds are currently unknown. However, seasonal, species and sex differences in these generators give rise to the differences in EFRs and FFRs reported here. At the peripheral level, birds have the capacity to regenerate hair cells after noise- or drug-induced damage (Corwin & Cotanche, 1988; Cotanche, Lee, Stone, & Picard, 1994; Dooling, Ryals, & Manabe, 1997; Stone & Cotanche, 2007). Furthermore, there is evidence to suggest that hair cells are produced in the cochlea of untraumatized adult birds (Ryals & Westbrook, 1990). Thus, seasonal variation in hair cell number may underlie differences in peripheral auditory processing. Seasonal and sex differences in auditory processing could also be mediated by hormones at the peripheral level. Oestrogen receptors have been identified in the inner ear of fish, mice, rats and humans (Hultcrantz et al., 2006; Sisneros et al., 2004). Furthermore, sex hormones are known to alter hearing processing in fish and mammals (Hultcrantz et al., 2006; Sisneros et al., 2004). Importantly, Noirot et al. (2009) identified oestrogen receptors in the cochlea of birds. Sensitivity to sex steroids in the cochlea could therefore lead to seasonal plasticity in peripheral auditory processing in birds.

Studies in mammals suggest EFR and FFR generators include auditory structures like the auditory nerve, cochlear nucleus and inferior colliculus (Kiren, Aoyagi, Furuse, & Koike, 1994; Kuwada et al., 2002). In songbirds, rapid onset of FFR and EFR suggests that major generators are in the brainstem or auditory nerve (Henry & Lucas, 2008). Furthermore, seasonal changes in auditory sensitivity in male white-crowned sparrows, *Zonotrichia leucophrys*, appear not to be mediated by changes in hair cell number or function (Caras et al., 2010). Therefore, seasonal plasticity in auditory processing in birds could also be mediated by variation at higher stages of the auditory pathway. For instance, different nuclei of the song control system in songbirds undergo seasonal variation in size, and these changes are associated with song production and learning (reviewed in Tramontin & Brenowitz, 2000). Similarly, differences in the relative size of auditory nuclei could lead to differences in auditory processing. Auditory nuclei in the hindbrain of birds with auditory specializations, like songbirds and owls, have relatively more cells (hyperplasia) than those of nonspecialists, like falcons and doves (Kubke, Massoglia, & Carr, 2004). Therefore, seasonal changes in the relative size of auditory nuclei could underlie seasonal differences in auditory processing. Sex hormones can also modulate the activity of auditory nuclei in the forebrain of birds (Maney & Pinaud, 2011; Yoder & Vicario, 2012), suggesting that seasonal plasticity may be due to hormonal influence on activity, rather than relative size, of auditory nuclei.

Sensory Physiology and the Organization of Mixed-species Flocks

A well-established hypothesis for the formation of mixed-species groups is that members gain fitness benefits associated with increased foraging efficiency and increased predator vigilance (Sridhar, Beauchamp, & Shanker, 2009). This hypothesis relies on an effective transfer of information, through cues or signals, both within and between species. Accordingly, several studies have shown that members of mixed-species groups respond appropriately to conspecific and heterospecific cues and signals associated with predator avoidance (Hetrick & Sieving, 2011; Templeton & Greene, 2007). Given the importance of information transfer, the use of heterospecific information has been recently proposed as a factor driving the organization of mixed-species groups (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Seppänen, Forsman, Mönkkönen, & Thompson, 2007). Goodale et al. (2010) proposed that the structure of mixed-species groups may depend on the differences among species in information gathering, production and transmission. Hence, differences (or similarities) among species in sensory physiology may be essential for how information transfer affects the structure of mixed-species groups. Furthermore, selection may favour the formation of mixed-species flocks between species with similar signal-processing mechanisms or the convergence of signal-processing mechanisms in members of mixed-species flocks.

Our study was not designed to evaluate whether auditory processing converges during the winter to a greater extent in species that form mixed-species flocks compared to species that only flock with conspecifics. To test this idea, it would be necessary to assess seasonal auditory plasticity in species that form mixed-species flocks and in species that do not. However, our results shed light on similarities and differences in auditory processing in three species that do form mixed-species flocks: nuthatches, titmice and chickadees (Morse, 1970; Nolen & Lucas, 2009). During the winter, when mixed-species flocks are formed, these species differ in how their auditory system processes the envelope and the temporal fine structure of sounds. Interestingly, EFRs and FFRs in nuthatches were similar or stronger than those of chickadees and titmice. This is somewhat unexpected given that nuthatches have the simplest vocal repertoire of the three species during the nonbreeding season. Their primary call is a repetition of a single harmonic stack with the strongest frequencies at about 2400 Hz and an AM rate of about 500–600 Hz. In contrast, chickadees and titmice have extraordinarily complex call systems involving a range of spectrally different elements. One possible explanation for the stronger EFRs and FFRs in nuthatches is that, given the simplicity of the nuthatch vocal repertoire, it is necessary for receivers to decode all information from spectral and temporal properties of conspecific note elements. Chickadees and titmice, with more complex call systems (Lucas et al., 2002), may encode more information in different elements of the calls and not in different dimensions of a single note type.

The rates of amplitude modulation in the nuthatch call and in the 'D' notes of the 'chick-a-dee' call of titmice and chickadees are between 500 Hz and 600 Hz (Freeberg, Lucas, & Clucas, 2003; Lucas et al., in press). In chickadees, however, there is variation in the structure of D notes. One variant has strong amplitude fluctuations and consists of two fundamentals, the harmonics of these fundamentals, and the distortion products from the interactions (Nowicki & Capranica, 1986). Another variant, the 'harsh D', has a noisier spectrum with less pronounced amplitude modulations around 500–600 Hz (Lucas & Freeberg, 2007; Smith, 1972). The type of information encoded in the amplitude envelope of chickadee, titmice and nuthatch calls, and how conspecifics and heterospecifcs use this information, is currently unknown. However, our results suggest that titmice and nuthatches may process the amplitude envelope of these vocalizations similarly. Furthermore, we have recently shown that titmice and nuthatches perform similarly when processing the amplitude envelope of three-tone harmonic stacks with frequency separations of 600 Hz (Lucas et al., in press). In contrast, our results suggest that chickadees may process nuthatch calls and chickadee and titmice D notes differently. During the winter, chickadees show weaker EFRs than titmice and nuthatches to sounds modulated at 500 Hz. One possibility is that chickadees rely less on the amplitude envelope of the calls, and

more on processing the spectral properties. Another possibility is that discrimination between D notes and harsh D notes (with weaker amplitude fluctuations around 600 Hz) is facilitated by an auditory system with less selectivity for amplitude fluctuations around that range of modulation frequencies. An auditory system that is highly sensitive to amplitude fluctuations could process very well the amplitude fluctuations in vocalizations with strong and weak envelope fluctuations, like the D and harsh D notes, respectively. On the other hand, an auditory system less sensitive to amplitude fluctuations would be more likely to process the strong envelope fluctuations in D notes, but not the weaker envelope fluctuations around 600 Hz of harsh D notes. Therefore, the weak EFRs in chickadees during the winter may reflect a mechanism to distinguish between the two types of notes.

Other studies have shown that these species differ during the winter in auditory sensitivity to high-frequency sounds (Henry & Lucas, 2008, 2010). The high-frequency limit of auditory sensitivity is higher in titmice and chickadees than in nuthatches (Henry & Lucas, 2010). In titmice, the sensitivity at high frequencies is consistent with the presence of high-frequency alarm calls in their vocal repertoire (Henry & Lucas, 2008; Lucas et al., in press). The difference in auditory sensitivity at high frequencies suggests that the active space of titmice alarm calls is larger for titmice, followed by chickadees, and much smaller for nuthatches. If chickadees and nuthatches benefit from predator avoidance in these mixed-species flocks, and heterospecific information plays an important role in flock structure, we would expect nuthatches to flock closer to titmice than to chickadees. This matches, to a great extent, the observed pattern in which titmice are nuclear species and facilitate flock formation and movement, while nuthatches are satellites and usually follow the flocks (Dolby & Grubb, 2000; Morse, 1970; Sieving, Contreras, & Maute, 2004).

Concluding Remarks

Overall, we show here that white-breasted nuthatches, tufted titmice and Carolina chickadees exhibit seasonal variation in auditory processing of the temporal fine structure and the amplitude envelope of sounds. Within species, we report sex differences in auditory processing during the breeding season, but not outside of the breeding season. These results suggest that males and females converge in auditory processing of communication signals during the winter, but diverge during the breeding season. Sexual selection on auditory processing of songs used for reproduction purposes may then be acting differently in males and females. Outside of the breeding season, species differences and similarities in auditory processing may affect the organization of chickadee–titmouse–nuthatch mixed-species flocks.

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Supplementary Material

Supplementary Material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2015.01.036.

References

Ball, G. F. (1999). The neuroendocrine basis of seasonal changes in vocal behavior among songbirds. In M. D. Hauser, & M. Konishi (Eds.), *The design of animal communication* (pp. 213–253). Cambridge, MA: MIT Press.

Basu, M., Krishnan, A., & Weber-Fox, C. (2010). Brainstem correlates of temporal auditory processing in children with specific language impairment. *Developmental Science, 13*, 77–91.

Bloomfield, L. L., Phillmore, L. S., Weisman, R. G., & Sturdy, C. B. (2005). Note types and coding in parid vocalizations. III: the chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Canadian Journal of Zoology, 83*, 820–833.

Boersma, P. (2001). Praat, a system for doing phonetics by computer. *Glot International, 5*, 341–345.

Boston, J. R., & Møller, A. R. (1985). Brainstem auditory evoked potentials. *Critical Reviews in Biomedical Engineering, 13*, 97–123.

Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland, MA: Sinauer.

Brenowitz, E. A. (2004). Plasticity of the adult avian song control system. *Annals of the New York Academy of Sciences, 1016*, 560–585.

Burton, M. J., Cohen, L. T., Rickards, F. W., McNally, K. I., & Clark, G. M. (1992). Steady-state evoked-potentials to amplitude modulated tones in the monkey. *Acta Oto-Laryngologica, 112*, 745–751.

Caras, M. L., Brenowitz, E., & Rubel, E. W. (2010). Peripheral auditory processing changes seasonally in Gambel's white-crowned sparrow. *Journal of comparative Physiology A, 196*, 581–599.

Catchpole, C. K., & Slater, P. J. B. (2008). *Bird song: Biological themes and variations*. New York, NY: Cambridge University Press.

Chandrasekaran, B., & Kraus, N. (2010). The scalp-recorded brainstem response to speech: neural origins and plasticity. *Psychophysiology, 47*, 236–246.

Christie, P., Mennill, D. J., & Ratcliffe, L. M. (2004). Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. *Behavioral Ecology and Sociobiology, 55*, 341–348.

Corwin, J. T., & Cotanche, D. A. (1988). Regeneration of sensory hair cells after acoustic trauma. *Science, 240*, 1772–1774.

Cotanche, D. A., Lee, K. H., Stone, J. S., & Picard, D. A. (1994). Hair cell regeneration in the bird cochlea following noise damage or ototoxic drug damage. *Anatomy and Embryology, 189*, 1–18.

Dolby, A. S., & Grubb, T. C. (2000). Social context affects risk taking by a satellite species in a mixed-species foraging group. *Behavioral Ecology, 11*, 110–114.

Dolphin, W. F., Au, W. W. L., Nachtigall, P. E., & Pawloski, J. (1995). Modulation rate transfer functions to low-frequency carriers in three species of cetaceans. *Journal of Comparative Physiology A, 177*, 235–245.

Dolphin, W. F., & Mountain, D. C. (1992). The envelope following response: scalp potentials elicited in the Mongolian gerbil using sinusoidally AM acoustic signals. *Hearing Research, 58*, 70–78.

Dooling, R. J., Lohr, B., & Dent, M. L. (2000). Hearing in birds and reptiles. In R. J. Dooling, R. R. Fay, & A. N. Popper (Eds.), *Comparative hearing: Birds and reptiles* (pp. 308–359). New York, NY: Springer.

Dooling, R. J., Ryals, B. M., & Manabe, K. (1997). Recovery of hearing and vocal behavior after hair-cell regeneration. *Proceedings of the National Academy of Sciences, 94*, 14206–14210.

Du, Y., Ma, T. F., Wang, Q., Wu, X. H., & Li, L. (2009). Two crossed axonal projections contribute to binaural unmasking of frequency-following responses in rat inferior colliculus. *European Journal of Neuroscience, 30*, 1779–1789.

Finneran, J. J., London, H. R., & Houser, D. S. (2007). Modulation rate transfer functions in bottlenose dolphins (*Tursiops truncatus*) with normal hearing and high-frequency hearing loss. *Journal of Comparative Physiology A, 193*, 835–843.

Fletcher, H. (1940). Auditory patterns. *Reviews of Modern Physics, 12*, 47–65.

Freeberg, T. M., Lucas, J. R., & Clucas, B. (2003). Variation in chick-a-dee calls of a population of Carolina chickadees, *Poecile carolinensis*: identity and redundancy within note types. *Journal of the Acoustical Society of America, 113*, 2127–2136.

Gall, M. D., Brierley, L. E., & Lucas, J. R. (2012a). The sender–receiver matching hypothesis: support from the peripheral coding of acoustic features in songbirds. *Journal of Experimental Biology, 215*, 3742–3751.

Gall, M. D., Henry, K. S., & Lucas, J. R. (2012b). Two measures of temporal resolution in brown-headed cowbirds (*Molothrus ater*). *Journal of Comparative Physiology A, 198*, 61–68.

Gall, M. D., & Lucas, J. R. (2010). Sex differences in auditory filters of brown-headed cowbirds (*Molothrus ater*). *Journal of Comparative Physiology A, 196*, 559–567.

Gall, M. D., Salameh, T., & Lucas, J. R. (2013). Songbird frequency selectivity and temporal resolution vary with sex and season. *Proceedings of the Royal Society B: Biological Sciences, 280*, 20122296.

Goense, J. B. M., & Feng, A. S. (2005). Seasonal changes in frequency tuning and temporal processing in single neurons in the frog auditory midbrain. *Journal of Neurobiology, 65*, 22–36.

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution, 25*, 354–361.

Goodale, E., & Kotagama, S. W. (2008). Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behavioral Ecology, 19*, 887–894.

Hall, J. W., III (2007). *Handbook of auditory-evoked responses*. Boston, MA: Allyn & Bacon.

Henry, K. R. (1997). Sharply tuned cochlear nerve ensemble periodicity responses to sonic and ultrasonic frequencies. *Journal of Comparative Physiology A, 181*, 239–246.
Henry, K. S., Gall, M. D., Bidelman, G., & Lucas, J. R. (2011). Songbirds trade off auditory frequency resolution and temporal resolution. *Journal of Comparative Physiology A, 197*, 351–359.
Henry, K. S., & Lucas, J. R. (2008). Effects of acoustic signal space on auditory sensitivity and temporal resolution in three songbirds. *Animal Behaviour, 76*, 1659–1671.
Henry, K. S., & Lucas, J. R. (2009). Vocally correlated seasonal auditory variation in the house sparrow (*Passer domesticus*). *Journal of Experimental Biology, 212*, 3817–3822.
Henry, K. S., & Lucas, J. R. (2010). Auditory sensitivity and the frequency selectivity of auditory filters in the Carolina chickadee, *Poecile carolinensis*. *Animal Behaviour, 80*, 497–507.
Hetrick, S. A., & Sieving, K. E. (2011). Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behavioral Ecology, 23*, 83–92.
Hillery, C. M. (1984). Seasonality of two midbrain auditory responses in the treefrog, *Hyla chrysoscelis*. *Copeia, 1984*, 844–852.
Hultcrantz, M., Simonoska, R., & Stenberg, A. E. (2006). Estrogen and hearing: a summary of recent investigations. *Acta Oto-Laryngologica, 126*, 10–14.
Kiren, T., Aoyagi, M., Furuse, H., & Koike, Y. (1994). An experimental study on the generator of amplitude-modulated following response. *Acta Oto-Laryngologica, 114*, 28–33.
Kubke, M. F., Massoglia, D. P., & Carr, C. E. (2004). Bigger brains or bigger nuclei? Regulating the size of auditory structures in birds. *Brain, Behavior and Evolution, 63*, 169–180.
Kuwada, S., Anderson, J. S., Batra, R., Fitzpatrick, D. C., Teissier, N., & D'Angelo, W. R. (2002). Sources of the scalp-recorded amplitude-modulation following response. *Journal of the Academy of Audiology, 13*, 188–294.
Lohr, B., Nowiki, S., & Weisman, R. (1991). Pitch production in Carolina chickadee songs. *Condor, 93*, 197–199.
Lucas, J. R., & Freeberg, T. M. (2007). Information' and the chick-a-dee call: communicating with a complex vocal system. In K. A. Otter (Ed.), *Ecology and behavior of chickadees and titmice: An integrated approach* (pp. 199–213). New York, NY: Oxford University Press.
Lucas, J. R., Freeberg, T. M., Egbert, J., & Schwabl, H. (2006). Corticosterone, body mass, and caching rates of Carolina chickadees from disturbed and undisturbed sites. *Hormones and Behavior, 49*, 634–643.
Lucas, J. R., Freeberg, T. M., Krishnan, A., & Long, G. R. (2002). A comparative study of avian auditory brainstem responses: correlations with phylogeny and vocal complexity, and seasonal effects. *Journal of Comparative Physiology A, 188*, 981–992.
Lucas, J. R., Freeberg, T. M., Long, G. R., & Krishnan, A. (2007). Seasonal variation in avian auditory evoked responses to tones: a comparative analysis of Carolina chickadees, tufted titmice, and white-breasted nuthatches. *Journal of Comparative Physiology A, 193*, 201–215.
Lucas, J. R., Peterson, L., & Boudinier, R. (1993). The effects of time constraints and changes in body mass and satiation on the simultaneous expression of caching and diet-choice decisions. *Animal Behaviour, 45*, 639–658.
Lucas, J. R., Vélez, A., & Henry, K. S. (in press). Habitat and vocal correlates of auditory evoked potentials to complex tones in four songbirds. *Journal of Comparative Physiology A*, http://dx.doi.org/10.1007/s00359-015-0986-7.
Maney, D. L., Cho, E., & Goode, C. T. (2006). Estrogen-dependent selectivity of genomic responses to birdsong. *European Journal of Neuroscience, 23*, 1523–1529.
Maney, D. L., & Pinaud, R. (2011). Estradiol-dependent modulation of auditory processing and selectivity in songbirds. *Frontiers in Neuroendocrinology, 32*, 287–302.
Marler, P. (2004). Bird calls: a cornucopia for communication. In P. Marler, & H. Slabbekoorn (Eds.), *Nature's music: The science of bird song* (pp. 132–177). San Diego, CA: Elsevier Academic Press.
Marler, P., & Slabbekoorn, H. (2004). *Nature's music: The science of bird song*. San Diego, CA: Elsevier Academic Press.
Moore, B. C. J. (1993). Frequency analysis and pitch perception. In W. A. Yost, A. N. Popper, & R. R. Fay (Eds.), *Human psychophysics* (pp. 56–115). New York, NY: Springer.
Morse, D. H. (1970). Ecological aspects of some mixed-species foraging flocks of birds. *Ecological Monographs, 40*, 119–168.
Nelson, D. A., & Marler, P. (1990). The perception of birdsong and an ecological concept of signal space. In W. C. Stebbins, & M. A. Berkley (Eds.), *Complex signals: Vol. II. Comparative perception* (pp. 443–478). New York, NY: J. Wiley.
Noirot, I. C., Adler, H. J., Cornil, C. A., Harada, N., Dooling, R. J., Balthazart, J., et al. (2009). Presence of aromatase and estrogen receptor alpha in the inner ear of zebra finches. *Hearing Research, 252*, 49–55.
Nolen, M. T., & Lucas, J. R. (2009). Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. *Animal Behaviour, 77*, 1137–1146.
Nowicki, S., & Capranica, R. R. (1986). Bilateral syringeal interaction in vocal production of an oscine bird sound. *Science, 23*, 1297–1299.
Offutt, G. (1965). Behavior of the tufted titmouse before and during the nesting season. *Wilson Bulletin, 77*, 382–387.
Owens, J. L., & Freeberg, T. M. (2007). Variation in chick-a-dee calls of tufted titmice, *Baeolophus bicolor*: note type and individual distinctiveness. *Journal of the Acoustical Society of America, 122*, 1216–1226.
Parthasarathy, A., & Bartlett, E. (2012). Two-channel recording of auditory-evoked potentials to detect age-related deficits in temporal processing. *Hearing Research, 289*, 52–62.
Popov, V. V., & Supin, A. Y. (1988). Auditory evoked responses to rhythmic sound pulses in dolphins. *Journal of Comparative Physiology A, 183*, 519–524.
Pyle, P. (1997). *Identification guide to North American birds*. Bolinas, CA: Slate Creek Press.
Ritchison, G. (1983). Vocalizations of the white-breasted nuthatch. *Wilson Bulletin, 95*, 440–451.
Ryals, B. M., & Westbrook, E. W. (1990). Hair cell regeneration in senescent quail. *Hearing Research, 50*, 87–96.
Seppänen, J. T., Forsman, J. T., Mönkkönen, M., & Thompson, R. L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology, 88*, 1622–1633.
Sieving, K. E., Contreras, T. A., & Maute, K. L. (2004). Heterospecific facilitation of forest-boundary crossing by mobbing understory birds in north-central Florida. *Auk, 12*, 738–751.
Simmons, A. M., & Buxbaum, R. C. (1996). Neural cues for 'pitch' processing in a unique vertebrate auditory system. In C. F. Moss, & S. J. Shettleworth (Eds.), *Neuroethological studies of cognitive and perceptual processes* (pp. 185–228). Boulder, CO: Westview Press.
Sisneros, J. A., Forlano, P. M., Deitcher, D. L., & Bass, A. H. (2004). Steroid-dependent auditory plasticity leads to adaptive coupling of sender and receiver. *Science, 305*, 404–407.
Smith, S. T. (1972). *Communication and other social behavior in* Parus carolinensis. Cambridge, MA: Nuttall Ornithological Club.
Smith, S. T. (1991). *The black-capped chickadee: Behavioral ecology and natural history*. Ithaca, NY: Comstock.
Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour, 78*, 337–347.
Stone, J. S., & Cotanche, D. A. (2007). Hair cell regeneration in the avian auditory epithelium. *International Journal of Developmental Biology, 51*, 633–647.
Templeton, C. N., & Greene, E. (2007). Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences of the United States of America, 104*, 5479–5482.
Thirakhupt, K. (1985). *Foraging ecology of sympatric parids: individual and population responses to winter food scarcity* (Doctoral thesis). West Lafayette, IN: Purdue University.
Tramontin, A. D., & Brenowitz, E. A. (2000). Seasonal plasticity in the adult brain. *Trends in Neuroscience, 23*, 251–258.
Tramontin, A. D., Hartman, V. N., & Brenowitz, E. A. (2000). Breeding conditions induce rapid and sequential growth in adult avian song control circuits: a model of seasonal plasticity in the brain. *Journal of Neuroscience, 20*, 854–861.
Van Tienhoven, A. (1983). *Reproductive physiology of vertebrates*. Ithaca, NY: Cornell University Press.
Viemeister, N. F., & Plack, C. J. (1993). Time analysis. In W. A. Yost, A. N. Popper, & R. R. Fay (Eds.), *Human psychophysics* (pp. 116–154). New York, NY: Springer.
Woolley, S. M. N., Gill, P. R., Fremouw, T., & Theunissen, F. E. (2009). Functional groups in the avian auditory system. *Journal of Neuroscience, 29*, 2780–2793.
Yoder, K. M., & Vicario, D. S. (2012). To modulate and be modulated: estrogenic influences on auditory processing of communication signals within a socio-neuro-endocrine framework. *Behavioral Neuroscience, 126*, 17–28.