Auditory sensitivity and the frequency selectivity of auditory filters in the Carolina chickadee, *Poecile carolinensis*

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Chickadees produce elaborate vocalizations, but their basic auditory capabilities remain unexplored. We used auditory brainstem responses to tone bursts to assess the auditory sensitivity of Carolina chickadees at frequencies from 0.5 to 8 kHz and the percentage of frequency selectivity (quality) of auditory filters at frequencies from 2 to 4 kHz. The high-frequency limit of sensitive hearing was relatively high in chickadees compared to other songbirds tested using the same method, while the low-frequency limit was similar among species. These results support a previously noted correlation across songbirds between the high-frequency limit of sensitive hearing and the maximum frequency of vocalizations. The frequency selectivity of auditory filters in chickadees increased with increasing frequency. Frequency selectivity was intermediate compared to other species at 2 and 3 kHz, and relatively high at 4 kHz. This pattern suggests that frequency selectivity is generally greatest within the frequency range of long-range communication signals, and maximum frequency selectivity may be greater in woodland species than in open habitat species. Greater frequency selectivity may have evolved for greater frequency resolution of vocal signals, which are relatively tonal in woodland species, or for better signal detection in noise. Finally, males had greater auditory sensitivity than females, whereas females had greater frequency selectivity than males. Greater frequency selectivity may enhance perception of the frequency difference between song notes, which indicates male quality in another chickadee species.

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Natural selection for efficient communication generally favours a close match between signal design and sensory capabilities (Endler 1992). Indeed, studies of communication systems reveal correlations between signal form and receiver physiology in a broad variety of taxa (e.g. insects: Lall et al. 1980; frogs: Feng et al. 2006; lizards: Nava et al. 2009). In other cases, however, the correlation may be disrupted by constraints acting on the sender or receiver (Ryan et al. 1990), or additional selective pressures acting on the sensory system (e.g. detection of prey; Konishi 1973). In songbirds, species differences in vocal communication signals are well documented (Nelson & Marler 1990), while differences in auditory capabilities are less explored. As a result, the extent to which auditory capabilities have diversified in parallel with vocal signals is not well understood.

In general, natural selection is expected to favour sensitive hearing across the frequency range of vocal signals. Estimates of auditory sensitivity are available for approximately 25 of 5000 songbird species (Dooling et al. 2000). Audiograms plotting auditory thresholds (minimum detectable sound pressure levels) as a function of frequency are broadly similar in these species, with best sensitivity from 2 to 3 kHz and moderate sensitivity (i.e. auditory thresholds within 30 dB of best sensitivity) between 0.5 and 6–8 kHz. A few species with relatively high-frequency vocal signals, however, are more sensitive to frequencies above 3–4 kHz (Konishi 1969, 1970; Okanoya & Dooling 1988; Langemann et al. 1998; Henry & Lucas 2008). The emerging pattern suggests that the high-frequency limit of sensitive hearing may coevolve with the maximum frequency of vocal signals in songbirds.

The peripheral auditory system of vertebrates performs a spectral decomposition of sound that determines the frequency resolution, or minimum detectable frequency difference, of the system. The system acts as an array of band-pass auditory filters, each representing a place on the sensory epithelium of the cochlea, that vary in centre frequency across the frequency range of hearing (Fletcher 1940; Moore 1993). Narrower filter bandwidth increases frequency resolution because signals of closely adjacent frequency are more likely to stimulate different filters. However, narrower bandwidth also decreases temporal resolution, or sensitivity to rapid changes in sound intensity. This is because bandwidth, in the frequency domain, and damping, in the time domain, are inversely

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related properties of a band-pass filter. For example, a narrower filter has lower damping, and therefore resonates for a prolonged period in response to a brief period of stimulation (like a tuning fork; reviewed in Viemeister & Plack 1993). In theory, tonal signals requiring precise frequency resolution are processed more effectively with narrow filters whereas modulated signals requiring greater temporal resolution are processed more effectively with broader filters (Viemeister & Plack 1993; Thyer & Mahar 2006). However, the extent to which auditory filters have coevolved with vocal modulation is not clear.

Studies of peripheral frequency selectivity in songbirds are largely limited to a few model species including the European starling, *Sturnus vulgaris* (Manley et al. 1985; Gleich 1994; Marean et al. 1998) and domestic canary, *Serinus canaria* (Lauer et al. 2009), or based on indirect methods such as critical ratios (Dooling et al. 2000). Frequency selectivity is commonly described in terms of the equivalent rectangular bandwidth (ERB; see Table 1 for abbreviations) of the auditory filter (i.e. the bandwidth of a rectangular filter with the same total area as the auditory filter), or %ERB, which is ERB expressed as a percentage of centre frequency. Taken together, these studies find that ERB increases with increasing frequency, while %ERB may decrease slightly. More recently, a comparative study of five species found that frequency selectivity may vary with habitat-based differences in the modulation rate of long-range signals (Henry & Lucas 2010). Woodland species, which tend to communicate with tonal signals, appear to have greater frequency selectivity than open habitat species, which tend to communicate using faster modulations.
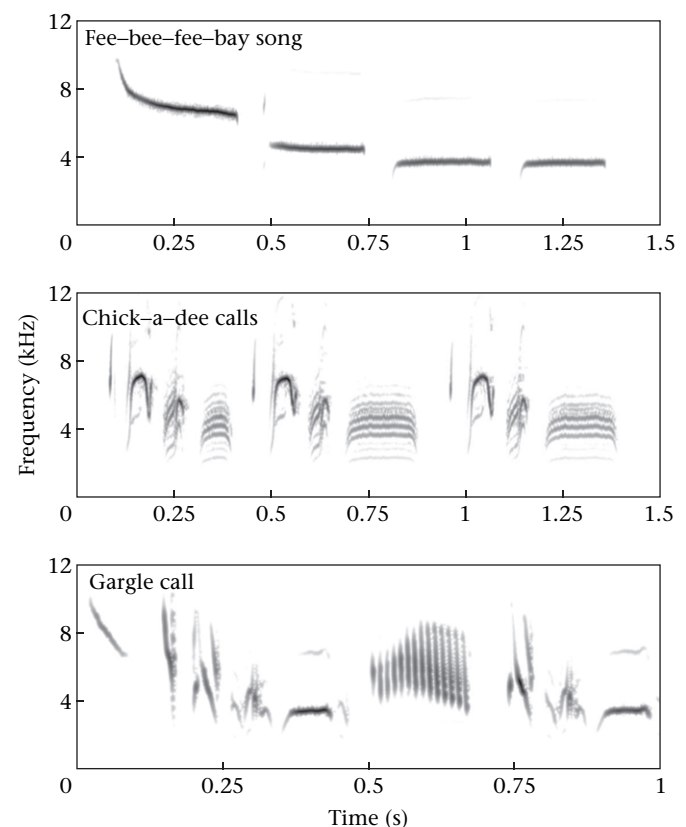
Several studies have used auditory brainstem responses (ABRs) to tone bursts to evaluate the frequency range of auditory sensitivity in songbirds (Woolley & Rubel 1999; Woolley et al. 2001; Lucas et al. 2007; Henry & Lucas 2008, 2009) and other small birds (Brittan-Powell et al. 2002; Brittan-Powell & Dooling 2004). ABRs are voltage waveforms recorded from the scalp that reflect action potentials generated within the cochlea and auditory brainstem nuclei (reviewed in Hall 2007). ABR waveforms consist of three to five voltage peaks occurring within 10 ms of stimulus onset. ABR amplitude is positively related to the number of neural responses and their synchrony, and hence, generally reflects the audibility of the stimulus. ABR latency, or the reaction time to the stimulus, is inversely related to the sensation level of the stimulus (i.e. dB above threshold), and hence generally decreases with increasing auditory sensitivity (Brittan-Powell et al. 2002). The ABR threshold is the lowest stimulus intensity that evokes a detectable response. ABR thresholds in birds are generally 25–30 dB higher than behavioural auditory thresholds (Brittan-Powell et al. 2002, 2005).

The frequency selectivity of auditory filters is commonly determined by measuring auditory thresholds in notched noise (reviewed in Moore 1993). Notched noise is white masking noise with a band of spectral energy, or notch, filtered out around a test frequency. Auditory thresholds are measured at the test frequency as the bandwidth of the notch is increased from zero. Auditory thresholds

decrease with increasing notch bandwidth, and in general, thresholds should decrease more rapidly when the auditory filter is narrower. The specific shape of the auditory filter can be derived from the relationship between the auditory threshold and notch bandwidth based on the power spectrum model of auditory masking (Fletcher 1940). Auditory filter shapes can be determined from behavioural auditory thresholds (e.g. Moore & Glasberg 1983; Marean et al. 1998) or from ABR thresholds (e.g. Henry & Lucas 2010).

North American chickadees are known to produce elaborate vocal communication signals, but their basic auditory capabilities are largely unexplored. Previous studies of the Carolina chickadee, *Poecile carolinensis* (Paridae) assessed sensitivity to clicks (Lucas et al. 2002) and tone bursts ranging in frequency from 1 to 4 kHz using ABR amplitude and latency (Lucas et al. 2007). Here, we examine auditory sensitivity over a broader range of stimulus frequencies (0.5–8 kHz) using not only ABR amplitude and latency, but also ABR thresholds. Furthermore, we examine the frequency selectivity of auditory filters from 2 to 4 kHz (i.e. within the frequency range of best sensitivity) using ABR thresholds in notched masking noise.

The Carolina chickadee is a small (10 g), nonmigratory, woodland songbird species (Monstrom et al. 2002). Individuals defend territories as breeding pairs during spring and early summer, but live in small flocks of two to eight birds outside of the breeding season. Vocalizations generally fall into three categories based on acoustic structure and function (Fig. 1; Smith 1972; Hailman 1989). Fee-bee-fee-bay songs contain four to five slowly delivered, tonal notes with little or no frequency modulation and average

Table 1
Commonly used abbreviations and definitions

ABR	Auditory brainstem response
AM	Amplitude modulation
ERB	Equivalent rectangular bandwidth; the bandwidth of a rectangular filter with the same total area as the auditory filter; 4 times centre frequency divided by p
FM	Frequency modulation
K'	Efficiency; the signal-to-noise ratio of the auditory filter in dB
%ERB	ERB of the auditory filter expressed as a percentage of centre frequency

Figure 1. Spectrograms of commonly produced Carolina chickadee vocalizations. Spectrograms were generated in PRAAT based on a Fourier transform of digital recordings (sampling rate = 44.1 kHz) with a 8.7 ms Gaussian analysis window and −3 dB bandwidth of 150 Hz. Fee-bee-fee-bay and chick-a-dee recording are from the Macaulay Library (recording 84817 by Wilbur L. Hershberger; www.macaulaylibrary.org). The gargle recording is from Elliot et al. (1997). Note the difference in timescale for the gargle vocalization.