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3pAB2. Reverberlocation in chickadees?

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Chickadee songs provide conspecifics with information about the locations of singers. Song amplitude, frequency, and reverberation all vary with distance, and it is thought that chickadees use such cues to estimate distance. The current study examined transmission of chickadee songs in an open field to assess whether other cues such as relative changes in inter-note timing or relative differences in spectral energy might also provide useful information about a singer's location. Surprisingly, the difference between direct signal energy and reverberant spectral energy provided clear indications of how far a song had traveled. Preliminary analyses suggest that this cue may be robust to variations in source level, note duration, note frequency, and transmission loss. If chickadees use this cue to judge auditory distance, then this may explain why they maintain specific spectral ratios between the notes within their songs. Specifically, the spectral spacing of notes within songs appears to be directly related to chickadee auditory filter bandwidth. We describe ranging of a singing chickadee based on the spectral profile of its songs as reverberlocation (construed as an instance of passive echolocation) because it involves comparisons between a direct signal and echoes of a signal.

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INTRODUCTION

Male black-capped chickadees (*Poecile atricapillus*) produce a two-note song (referred to as the ‘*fee-bee*’ song) when defending their territories and when attempting to attract mates (Ficken, 1981; Smith, 1991). Both functions require that listening birds be able to judge the position of the singer. Often, visual information is insufficient to reveal a singer’s location, especially in the forested habitats where singers are most likely to be found. Consequently, acoustic cues within a received song may provide the only means whereby a listening bird can localize a singer. In the case of territory defense, in particular, it is critical that listeners be able to judge their distance from a singer, because otherwise they would only be able to tell that they are encroaching upon another bird’s territory, or being encroached upon themselves, through visual detection of a singer. Thus, for chickadee songs to be an effective deterrent to intruding males, it is important that they enable listeners to identify the spatial boundaries that a singer is likely to actively defend.

Birds are known to use several different cues to estimate their distance from singers (reviewed by Naguib & Wiley, 2001). It is not yet known which cues are most salient to chickadees. Evidence from playback studies (Shackleton *et al.*, 1992) as well as laboratory studies (Phillmore *et al.*, 1998) shows that chickadees do distinguish variations in sounds that could provide information about a singer’s distance. However, Fotheringham and Ratcliffe (1995) found that male chickadees did not respond differentially to playbacks of songs that had or had not been degraded to simulate transmission over different distances. They concluded from this result, and from consideration of the heterogeneity of habitats within which chickadees sing, that the *fee-bee* song might be difficult for listening birds to localize, and that the acoustic cues that birds normally use to localize singers might be insufficient for localizing a chickadee’s *fee-bee* song.

The acoustic features of the *fee-bee* song (Figure 1a) are consistent with use as a long-range communication signal. The frequencies used by individual singers vary within a relatively narrow band between 3.0-4.5 kHz and the duration of a song is generally about 1 s (Fotheringham & Ratcliffe, 1995; Hoeschele *et al.*, 2010). *Fee-bee* songs are audible to humans at distances of at least 80 m (Christie *et al.*, 2004). Because of the simple tonal structure of the notes within the song, there is relatively little degradation of signal features after transmission over this distance (Figure 1b). Although the frequencies within individual notes can vary within and across birds, a notable feature of the *fee-bee* song is that the ratio of frequencies of the two notes is relatively invariant (Horn *et al.*, 1992; Weisman *et al.*, 1990). In previous sound transmission experiments examining how the *fee-bee* song varied with distance (Fotheringham & Ratcliffe, 1995; Christie *et al.*, 2004), it was noted that: (1) temporal spreading associated with reverberation effectively increased the duration of each note and decreased the internote interval; (2) distortion associated with reverberation increased the variability of amplitude modulation in both notes and decreased the similarity of the received song to the song at the source; (3) frequency-dependent attenuation did not differentially impact the two notes within the song or the beginning or end of the *fee* note, which spans a greater range of frequencies than the *bee* note. Temporal distortions associated with reverberation were systematically related to distance, such that they could potentially provide information about the range of a singer. However, use of such cues by listeners would require exquisite temporal resolution and discrimination abilities as well as information about the temporal properties of the song at the source. Furthermore, the measures reported by Fotheringham and Ratcliffe suggest that in forested habitats, temporal distortions are non-monotonic with distance such that the temporal cues indicating that a song had traveled 100 m also indicated that a song had traveled 20 m. Consequently, to the extent that listening chickadees are able to determine the distance to singers, they are unlikely to do so based on frequency-dependent attenuation or temporal distortion cues.

RELATIVE SPECTRAL DIFFERENCES AS A CUE TO DISTANCE

Figure 1b shows a spectrographic representation of a recording of a *fee-bee* song that traveled 80 m in an open field. A surprising feature of this received signal is the presence of long-duration reverberant tails associated with each note of the song. In an open field, the main contributor to reverberation is reflection from the ground. Compared to a forested habitat, an open field is much less likely to generate strong reverberation. The extent to which notes reverberate in this environment raises the possibility that the notes within the *fee-bee* song are conducive to reverberating. Given that most of the spectral energy within the *fee-bee* song is focused within narrow spectral bands, reverberation would tend to supplement the direct signal, possibly extending the distance at which a song remains detectable.

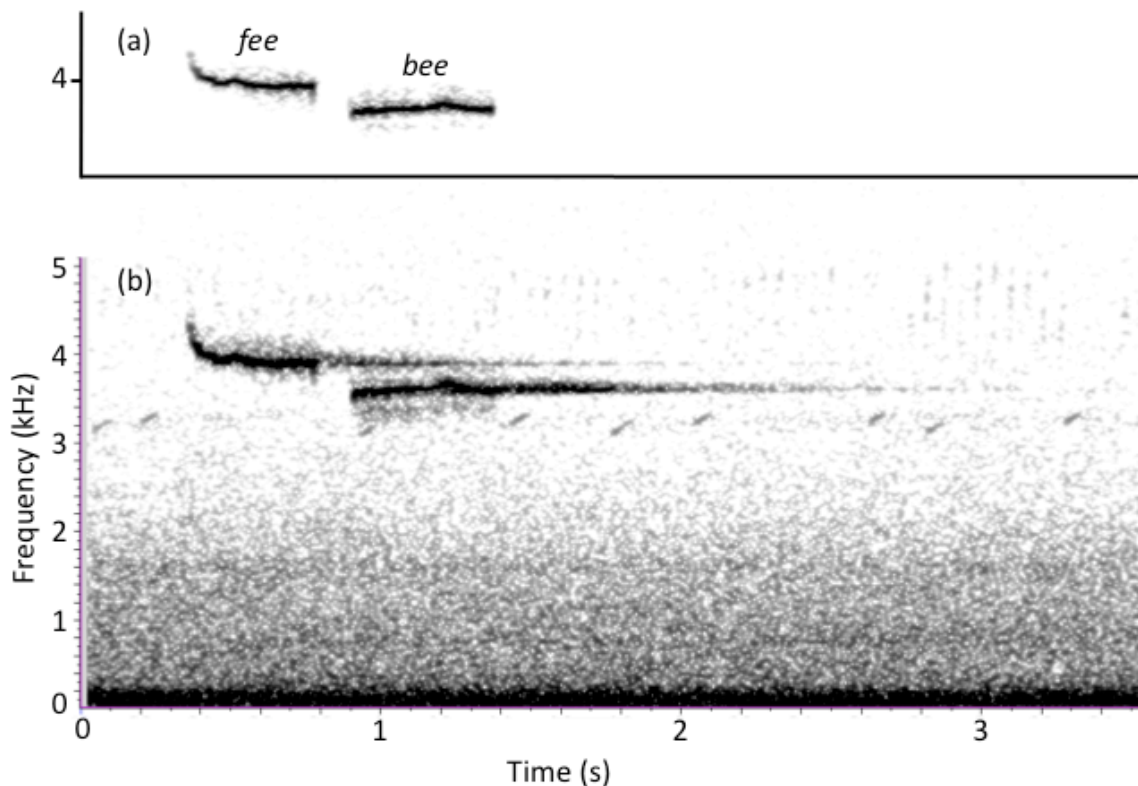


FIGURE 1. A *fee-bee* song produced by a black-capped chickadee recorded (a) at the source, and (b) from a distance of 80 m in an open field. Note that many of the detailed spectrotemporal features of the original signal are still evident at 80 m and that the duration of reverberant tails for each note is comparable to the duration of the entire song (FFT=2048, 98% overlap; Hanning window).

The reverberant tails evident at 80 m were also detectable at shorter distances. For all distances assessed (range 10 - 80 m), reverberant tails generated by the *fee* note extended throughout the duration of the *bee* note. Although such extended reverberation has not been explicitly noted in prior studies of chickadee songs, Fotheringham and Ratcliffe (1995) reported that reverberant tails from broadcast *fee* notes within songs extended at least 300 ms into the *bee* notes at distances of 50-80 m in forested habitats. It is important to note that the visibility of such reverberant tails in spectrographic representations of recorded songs is highly dependent on the parameter settings chosen (as well as ambient noise levels), and that use of default settings or settings chosen to display features of the source signal may render such tails invisible. Additionally, although the presence of reverberation is aurally detectable in recordings, the extended reverberant tail of the *fee* note is not aurally salient after the *bee* note begins. Finally, the low ambient noise levels present in a man-made open field may be especially conducive to the detection of broadcast-generated reverberation in spectrograms when parameters are selected to enhance the visibility of lower-level signals.

The protracted reverberant tails from the initial *fee* note effectively transform tonal *bee* notes into a non-harmonic, two-tone signal at the receiver; this is clearly evident in spectral analyses of the *bee* note received at a distance of 80 m (Figure 2a). Inspection of spectral peaks of *bee* notes revealed that as distance from the source decreased, the difference between the spectral energy contributed by each of the two tones increased (Figure 2, b-d). Assuming that singing chickadees produce *fee-bee* songs at relatively consistent source levels, the difference between the spectral peaks of the reverberant *fee* and the directly received *bee* note would provide an indication of the distance a song has travelled that is relatively independent of the song source level as well as the specific frequencies present within each note of the song. In other words, these spectral energy differences provide a relative cue to source distance that does not require comparisons with source features. For example, a *bee* note containing peaks at 3.8 and 4 kHz, produced at a source level of 80 dB, might produce a difference in spectral peaks of 35 dB at 20 m. If the singer shifted to a lower band, such that the spectral peaks were now at 3.3 kHz and 3.5 kHz, and

increased his source level to 85 dB, the spectral difference corresponding to a range of 20 m would still be 35 dB. Recent analyses of amplitude features of *fee-bee* songs (Hoeschele *et al.*, 2010) suggest that singing chickadees produce notes in which the ratio of spectral energy across notes is relatively stable, as would be necessary for spectral energy differences to provide reliable cues to distance.

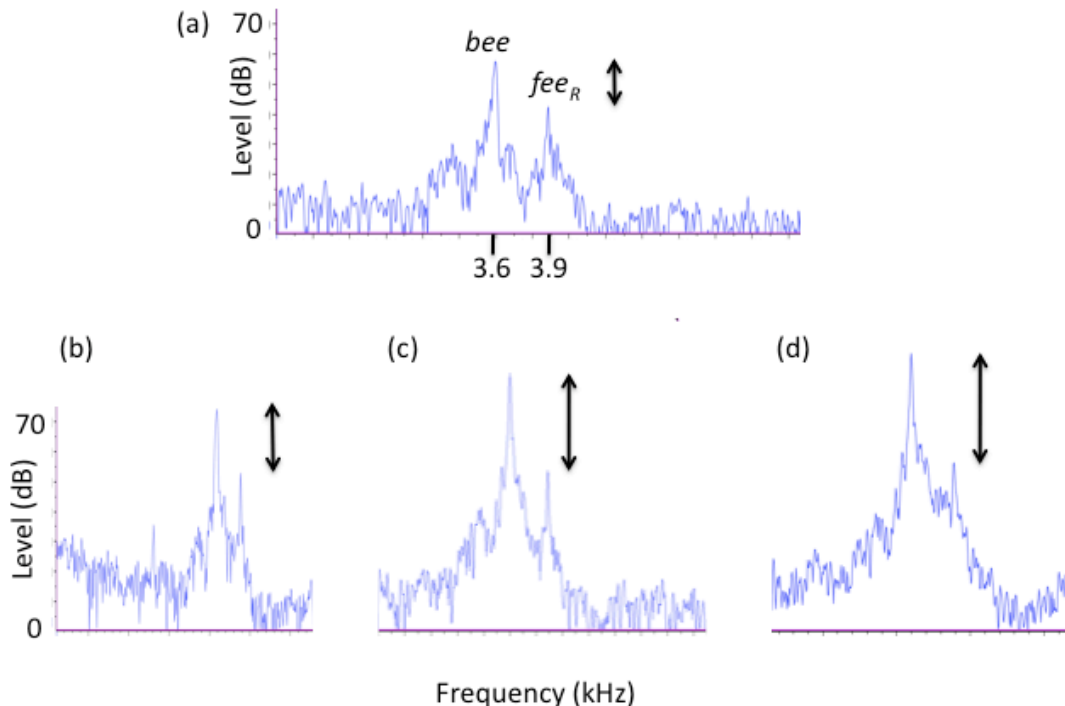


FIGURE 2. Spectra from segments of a *bee* note recorded at various distances. (a) A *bee* note received from a distance of 80 m shows a peak at 3.6 kHz corresponding to the directly received *bee* note, as well as a peak at 3.9 kHz (fee_R) generated by the reverberant tail from the preceding *fee* note (b, c, and d) show this same *bee* note received at 60, 40, and 20 m respectively. At closer ranges, the difference between the energy in each peak (denoted by arrows) is greater. Thus, it is possible to estimate the distance a song has travelled based on the difference between the two peaks regardless of their absolute levels or the specific frequencies that generate the two peaks. (FFT=8000, 98% overlap; Hanning window).

LOCATING SINGERS THROUGH REVERBERLOCATION

The most exquisitely sensitive mechanism for spatial hearing currently known in animals is echolocation. Animals that echolocate (e.g., bats and dolphins) typically extract information from a discrete stream of echoes generated by the sonar signals that they produce. Echolocation is traditionally described as an active process in which an individual emits signals and then listens for echoes generated by those signals to garner information about environmental conditions, most notably the locations and identities of various objects of interest. There are some indications that animals can also engage in passive echolocation, however. For instance, experiments have shown that a bottlenose dolphin can identify targets using a second dolphin's echolocation signals (Xitco & Roitblat, 1996). Bats can silently shadow a second echolocating bat that is attempting to capture a target, and then steal the target before the echolocating bat reaches it (Chiu *et al.*, 2008). Passive echolocation appears to be comparable to active echolocation in all respects other than the source of the sonar signal.

Consider now the situation faced by a chickadee attempting to ascertain the position of other singing chickadees. Like echolocating animals, a listening chickadee is in need of spatial information that can potentially be obtained through the auditory modality. Singing chickadees are producing signals to impact the actions of other birds. The notes that singers produce will generate echoes, but singers are unlikely to receive or detect most of these echoes or to obtain useful information from any echoes received. In contrast, listening birds will hear the direct signal as well

as many resulting echoes (the consequent reverberation). Unlike passively echolocating bats and dolphins, listening birds are unlikely to discern much about the environment from the echoes they receive. Nevertheless, listeners can potentially benefit from processing both direct signals and the echoes generated by those signals. In particular, by comparing the properties of directly and indirectly received signals, a listening chickadee can potentially gain spatial information about targets of interest (in this case singing chickadees) that would not otherwise be available (Nelson & Stoddard, 1998). A listening chickadee that compares reverberant echoes with direct signals to estimate auditory distances could thus be viewed as engaging in a form of passive echolocation. The main differences between this mode of spatial hearing and the kinds of passive echolocation used by dolphins and bats are that in the case of listening chickadees the receiver would not be near the origin of the direct signal, and that the stream of echoes being received would be effectively continuous rather than separated by silent intervals. Neither of these factors precludes the possibility of passive echolocation. We refer to this hypothetical spatial hearing process as *reverberlocation* to distinguish it from more conventional forms of active and passive echolocation that have been experimentally demonstrated, as well as processes in which reverberation-generated distortions of signal features are used to assess auditory distance. A listener that is reverberlocating compares a stream of reverberant echoes to a direct signal in order to obtain information about the position of the vocalizer. In the current context, reverberlocation is speculated to be a possible ranging mechanism used by a territorial songbird, but in principle the process could be used by any species that vocalizes at relatively long ranges in reverberant environments.

Preliminary analyses from recordings like the ones illustrated in Figures 1 and 2 have shown that reverberlocation of singing chickadees is technologically feasible (unpublished data), at least in an open field with low ambient noise levels. At a minimum, measurement of such cues may potentially provide a way for researchers to (1) automatically estimate the distances of non-visible singing chickadees in real-time without needing an extended array of stationary sensors, or (2) map out the effective acoustic territorial boundaries of a singer. Given that the forested habitats frequented by chickadees are more reverberant than an open field (Fotheringham & Ratcliffe, 1995), one would expect that spectral difference cues would continue to be a useful in natural habitats, although this has yet to be established.

Assuming that reverberant tails comparable to the ones shown in Figure 1 are also present in natural contexts, an obvious question is whether listening chickadees are themselves capable of reverberlocating singers. In order to use the kinds of spectral differences identified above to range singers, a listening chickadee would need to be able to resolve the spectral bands associated with *fee* and *bee* notes, to discriminate differences in energy levels within those bands, and to assess disparities in the levels within the two bands. Intriguingly, the ratio between the frequencies within *fee* and *bee* notes (which, as noted above, is relatively invariant within and across singers) closely matches the electrophysiologically-estimated spacing between a chickadee's auditory filters (Henry & Lucas, 2010). In other words, the frequencies produced within *fee-bee* songs appear to be separated by the minimal amount necessary to activate two adjacent auditory filters. Researchers have previously hypothesized that the stable ratio of note frequencies used by singing chickadees functions primarily as a species identifier (Weisman & Ratcliffe, 2004). If chickadees are reverberlocating, however, then this suggests that the ratio may reflect constraints on listeners' abilities to compare spectral differences after songs have travelled relatively long distances. If frequencies within the *fee-bee* song were spaced farther apart, then frequency-dependent attenuation might confound interpretation of spectral level differences, because the higher frequency band will typically attenuate more rapidly with distance. If the frequencies within the song were closer together, then the energy from the two bands would likely be integrated by the chickadee's auditory system, making spectral level comparisons impossible. The currently available evidence thus appears to be consistent with the possibility that chickadees could reverberlocate, and seems to suggest that the structure of *fee-bee* songs may be specifically adapted for this purpose.

CONCLUSION

It is well established that black-capped chickadees use their songs to influence the spatial locations of listeners spread across a region of forest that extends beyond the range of reliable visible detection. How chickadees accomplish this remains unclear. Past sound transmission experiments led researchers to suggest that chickadee songs are not well suited for providing information about the location of a singer (Fotheringham & Ratcliffe, 1995). That conclusion was based on the assumption that listening chickadees would need to compare absolute features of a received song to known properties of the source song to identify components that had been distorted or lost during transmission. We suggest here that relative cues based on comparisons of spectral energy within directly and indirectly received notes can provide a robust indicator of source distance that does not require knowledge of source features or the detection of distortions. We speculate that the structure of chickadee songs may be adapted to

facilitate use of such relative cues, and that listening chickadees may range singers through a process we refer to as *reverberlocation*.

Whether chickadees or other species that vocalize in reverberant environments use reverberlocation to obtain information about the positions of vocalizing conspecifics is an important question for future research. Even if it is determined that animals are not capable of naturally reverberlocating, this does not preclude the possibility that humans could develop new technologies for artificially reverberlocating vocalizing animals, which could facilitate future studies of animal bioacoustics.

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