Auditory distance assessment of singing conspecifics in Carolina wrens: the role of reverberation and frequency-dependent attenuation

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Abstract. Studies of auditory distance perception in songbirds have shown that the overall degradation of songs during atmospheric propagation can be used to estimate the distance of the singer (called ranging). Natural sound degradation, however, incorporates several additional auditory distance cues that are not always equally available. This study investigated whether Carolina wrens, Thryothorus ludovicianus, can separately use reverberation and high-frequency attenuation to estimate the distance of a singer. In response to playback, 40 m away from its singing location, subjects approached more frequently and responded more intensively to playback of clear (unattenuated) songs than to playback of reverberated, high-frequency attenuated, or naturally degraded songs. The results indicate that Carolina wrens can use reverberation and high-frequency attenuation separately to assess the distance of a singing conspecific. This ability could be an adaptation that enables them to defend territories efficiently in habitats with different acoustical properties. In addition, the ability to use several cues to assess auditory distance is likely to increase the accuracy of ranging by pooling information acquired in different ways.

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clear songs with the Audiomedia software and re-recorded through the Krohn-Hite filter (1–10 kHz) on the Marantz tape-recorder.

I produced tapes of reverberated songs by broadcasting and re-recording clear songs in a large attic (35 x 15 m), which provided multiple reflecting surfaces without producing irregular amplitude fluctuations or high-frequency attenuation. Compared to electronic reverberation, which adds regularly spaced echoes, a complex reverberation chamber provides more natural reverberation. I adjusted the positions of microphone (Sennheiser K3U/ME60) and loudspeaker (Realistic horn speaker, frequency response 1.5–2.5 kHz ± 2 dB, 2.5–8 kHz ± 3 dB) to ensure that the reverberation time of a 25-ms 3-kHz sine-wave tone matched that of the same tone broadcast through 50 m of deciduous forest in leaf at the Mason Farm Biological Reserve. I then generated reverberated songs by playing back and re-recording the clear songs with these microphone and loudspeaker positions (5 m apart). Although any such treatment influences the spectral composition of the signal to some degree, there was no indication of high-frequency attenuation (Fig. 2). A linear regression of the peak values (in dB) taken within every 500-Hz frequency band showed significant changes with increasing frequency compared to clear songs only for high-frequency filtered and naturally degraded songs, but not for reverberated songs (reverberated songs: r = 0.126; high-frequency attenuated songs: r = 0.840; naturally degraded songs: r = 0.609, N = 104).

Playback

Playback sessions were conducted during 21 April–12 May 1993 between 0630 and 1100 hours. This time interval avoided the dawn chorus and reduced confounding influences on responses later in the day (Shy & Morton 1986). Each of the 12 subjects received four treatments in a randomized order: (1) clear (unaltered) song (C), (2) reverberated song (R), (3) high-frequency attenuated song (F), and (4) naturally degraded song (D), (Fig. 1).

Because the objective of this study was to test whether the subjects could use the cues provided to estimate the distance of the loudspeaker, I used a relatively short playback period to reduce the subjects' ability to localize the position of the loudspeaker by using repeated cues during approach. Each playback tape contained only five songs of a neighbour, with silent intervals of about 3 s, the natural rate of singing by Carolina wrens. To control for any differences between different song types, each subject received a song of a different type. Carolina wrens have repertoires of about 30 discrete song types, but a singing male repeats each song type for a long time (often more than 100 times) before it switches to another song type (Morton 1982; Simpson 1982; personal observation).

For each of the four playback sessions with a subject, I placed the loudspeaker at about the same position on the side of the territory near the neighbour whose songs were used for playback. I used only songs from neighbours that I had not observed in repeated boundary disputes with the subjects while mapping the territories. I used songs of most subjects in playback to another subject. At least 2 days elapsed between trials with the same subject, and at least 24 h lapsed between trials with immediate neighbours. To identify the location of the subject prior to each trial and to reduce individual differences in motivation, I started the playbacks after the subject had sung at least four songs and when the neighbour whose songs were used for playback was silent. Another precondition for starting a playback was that the subject was not counter-singing with another neighbour. I taped the loudspeaker to a tree at a height of about 1.8 m, 40–60 m away from the subject but 10–20 m inside the boundary. I broadcast the playback at an intensity of 86 dB at 1 m (determined with a Realistic sound-level meter, C-weighting, fast response) which is within the amplitude range of singing Carolina wrens. I played the songs on a Marantz PMD 221 tape-recorder connected to a Perma Power S-722 amplifier and the Realistic horn loudspeaker mentioned above.

Response Measures

The primary response measure was approach distance, because Carolina wrens naturally approach intruders but do not approach distant singing conspecifics. This behaviour indicated most clearly that the subjects estimated that the simulated rival was within their territory. Because of the short playback periods, the subjects rarely attacked the loudspeaker or showed aggressive responses in its vicinity. I thus based additional
number of songs within 30 min following the playback.

A strong response, as determined from preliminary experiments, generally included longer latencies to resume singing, longer first singing bouts, and more songs within 25 m and 30 min following the playback. It also included an approach within 25 m of the loudspeaker, fewer songs within 15 min following the playback, and fewer singing bouts within 30 min following the playback. In summary, a strong response was indicated by a silent approach followed by a long singing bout.

**Statistical Analysis**

One playback of reverberated songs was excluded from the analysis because of technical problems during the playback. I then used a Wilcoxon matched-pairs signed-ranks test to compare differences between treatments in the main measure of response, the approach.

Because all response measures correlated with each other, I used a principal component analysis to extract one composite measure for each trial (McGregor 1992). This analysis used the first six response measures given above, because the seventh, the number of songs within 30 min following the playback, was not available in three trials. I then used the scores on the first principal component as the dependent variable in an analysis of variance. Finally, to test differences between treatments, I used the principal component scores in Wilcoxon matched-pairs signed-ranks tests (Sokal & Rohlf 1987).

To examine influences of temporal and spectral characteristics of a song on the response strength, I measured the length of the shortest silent interval between elements that contained the same frequencies (Fig. 1), the highest frequency and the dominant frequency (Fig. 2) in the clear version of each song type. I also measured the length of silent intervals between elements on the real-time spectrum analyzer, and I obtained the frequency measurements from averaged frequency spectra of songs with an accuracy of 80 Hz. The highest frequency was measured in a spectrum in which the amplitude of the dominant frequency was adjusted to the same level for all song types. I tested influences of these physical characteristics of song types on approaches with Mann-Whitney U-tests, and their influences on overall responses (first principal component scores) with linear regressions.

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**RESULTS**

**Comparisons of the Separate Response Measures**

The subjects stopped singing immediately after the playback started in 38 of the 47 trials (Fig. 3). Three of the five trials in which subjects continued singing involved the same individual. Eleven of the 12 subjects approached within 25 m of the loudspeaker in response to playback of clear songs, and four subjects approached playback of naturally degraded songs. Six subjects approached reverberated songs, and five approached high-frequency attenuated songs (Wilcoxon matched-pairs signed-ranks test: C: one-tailed $P=0.036$, C: F: one-tailed $P=0.007$, C: D: one-tailed $P=0.01$, R: F: two-tailed $P=0.075$, R: D: two-tailed $P=0.014$, F: D: two-tailed $P=0.054$; R-treatment: $N=11$, C: F, D: treatments: $N=12$ each). Thus, the subjects' approaches indicated that they discriminated only between playback of clear and degraded songs, but not between the different kinds of degraded songs.

The six vocal response measures were also consistently stronger following playback of clear songs than following playback of degraded songs (Fig. 4). In response to playback of clear songs, subjects had longer latencies to resume singing and sang fewer songs within 15 min, but sang more songs within 30 min following the playback. They also sang fewer bouts, but more songs within
their first bout, and more songs within 25 m of the loudspeaker (Fig. 4).
I also tested whether the highest and dominant frequencies of song types presented to subjects that approached playback of high-frequency attenuated or naturally degraded songs differed from song types presented to individuals that did not approach in response to these treatments. This analysis yielded no significant differences between song types (Mann-Whitney U-test: F-treatments: highest frequencies, P=0.513; dominant frequencies, P=0.807; D-treatments: highest frequencies, P=0.104; dominant frequencies, P=0.798, N=12).

Reverberation impairs discrimination between consecutive elements with the same frequencies. Therefore I tested whether the shortest silent interval between such elements differed between song types presented to subjects that did and did not approach reverberated and naturally degraded songs. This analysis showed no significant differences in the length of these intervals between song types (Mann-Whitney U-test: R-treatments: P=0.522, N=11; D-treatments: P=0.932, N=12). Thus, the results provided no evidence that these physical characteristics of a song influenced whether subjects approached playback of degraded songs.

Principal Component Analysis

Correlations between measures of response strength ranged from r=0.96 to 0.63. The response measures contributed about equally to the first principal component (Table I), which explained 43% of the variance in the responses. The second and third components explained an additional 22% and 17% of variance, respectively. Consequently, only scores on the first component were analysed further. An analysis of variance, with the scores on the first principal component as the dependent measure, showed significant influences of treatment and song types on the response strength. Neither order nor the interaction between order and treatment had a significant influence on the response strength (Table II). A pair-wise comparison of the response scores yielded significant differences between responses to playback of clear songs and all three kinds of degraded songs (Fig. 5, Table III). There were no significant differences between the responses to playback of reverberated, high-frequency attenuated and naturally degraded songs (Table III). The simple linear regressions showed an increase in response strength with increasing highest and dominant frequencies of song types, but the slopes were not significant (r=0.234 and r=0.161, respectively; N=47). There was no significant correlation between these two frequency measures.

DISCUSSION

The results indicate that Carolina wrens can use either reverberation or high-frequency attenuation of a song to estimate the distance of a conspecific singer. Both the subjects’ approaches and the overall responses showed that subjects responded differently to playback of reverberated, high-frequency attenuated and naturally degraded songs compared to playback of clear songs. The results are consistent with field observations that Carolina wrens cease singing and approach singing intruders but do not approach distant singing conspecifics. They also confirm Richards’ (1981) demonstration that Carolina wrens respond differently to playback of naturally degraded and clear songs when played with the same amplitude within a subject’s territory.
All prior range experiments have used playback periods long enough to elicit a close approach to the loudspeaker by the subjects (Richards 1981; McGregor et al. 1983; McGregor & Falls 1984; McGregor & Krebs 1984; Shy & Morton 1986; Brindley 1991). This protocol had the advantage that the response strength of the subjects close to the loudspeaker could be observed. These prolonged playbacks, however, had the disadvantage of allowing the subjects to locate the actual position of the loudspeaker. The short playback period in this study reduced this problem, because no subject approached the loudspeaker during playback.

Because degradation of a song, in addition to providing cues for ranging, is likely to impair its detection or recognition (Richards 1981; Wiley & Richards 1982; Wiley 1994), there are at least two explanations for the differences in response: (1) the birds did not detect the reverberated, high-frequency attenuated and naturally degraded songs, or did not recognize them as conspecific; (2) the birds recognized all playbacks as conspecific but responded differently with regard to the advantage of the distance of the source of the song. The observation that subjects stopped singing immediately after the playback began in almost all trials indicates that they quickly detected and recognized the playbacks as conspecific.

In addition, the most obvious degradation features that cause a signal to reverberate, such as dense vegetation, do not change rapidly. No evidence yet documents the accuracy, however, with which birds can use reverberation of a song to estimate a singer’s distance. Very fine resolution is presumably difficult, because the degree of a signal’s reverberation depends on the specific properties of the actual transmission path. To judge distance by reverberation a receiver could either assess reverberation time in general, for instance by assessing the reverberation tail at the end of a song, or it could assess the degree of reverberation by using a standard, such as the silent intervals between elements with the same frequencies. Because the length of the silent intervals between such elements is usually small, there was a strong approach by the subjects, birds might have assessed reverberation without using these intervals as a standard. On the other hand, the increase in overall strength of response with an increase in length of the study might have resulted from increased conspecific activity (Becker 1982). In addition, a study of the relationship between animal behavior and the degree of reverberation (Morton 1975; Marten & Marler 1977). Thus, the results also indicate that Carolina wrens can use the relative intensities of high frequencies in received songs to assess the distance of the singer. This ability complements the use of reverberation for ranging. During winter, when trees carry no leaves and when reverberation in forests is low (Richards & Wiley 1980), reverberation alone might not provide enough information to assess the distance of a signal. Also, when territories are established in a complex environment, such as the area in this study, the degree of reverberation might be a more useful cue than the overall strength of the signal.

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