

## 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 potential 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 playbacks broadcast from within a subject's territory but at least 40 m away from its singing location, subjects approached more frequently and responded more intensely to playback of clear (unaltered) 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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One function of territorial bird song is to indicate the occupation of a territory (Krebs et al. 1978; Kroodsma & Byers 1991). Because male territorial songbirds are usually spaced far apart, their songs propagate over long distances before they reach a listening male conspecific. During propagation, songs progressively attenuate and degrade and thus provide potential cues about the distance of the signaller (Wiley & Richards 1978, 1982; Morton 1982, 1986). The ability to use auditory cues to estimate the distance of a singing conspecific (called ranging) could increase the efficiency of defending a territory: a bird that can assess the distance of a singing conspecific just by listening would only need to interrupt its other activities when a rival has actually intruded into its territory.

Although the overall amplitude of acoustic signals such as bird songs attenuates during propagation, the amplitude does not always reliably indicate the distance of the signaller. Signal ampli-

tude can be considerably influenced by the sender and weather conditions, so it does not always change predictably with increasing distance (Michelsen 1978; Wiley & Richards 1978). A bird would thus do better to estimate the distance of a singing conspecific by assessing degradation of the song independently of amplitude. Several studies have shown that male territorial birds respond less aggressively to playback of naturally degraded songs than to playback of clear (undegraded) songs when both are played with the same amplitude from the same location within the territory (Richards 1981; McGregor et al. 1983; McGregor & Falls 1984; McGregor & Krebs 1984). These results indicate that birds in fact perceive naturally degraded songs as coming from further away.

The degraded songs used in these experiments were produced by playing back and re-recording songs over 50–200 m in the subjects' natural habitat. Because naturally degraded songs can incorporate several potential cues for auditory distance estimation, such as (1) reverberation, (2) irregular amplitude fluctuations and (3) frequency-dependent attenuation (Wiley & Richards 1978, 1982), subjects could have used any of these cues

or a combination of them to estimate the distance of the simulated rival. These potential cues, however, depend differently on environmental influences, and thus are not always equally available. High frequencies in bird songs attenuate more rapidly than low frequencies in all habitats (Morton 1975; Marten & Marler 1977; Piercy et al. 1977). Turbulence caused by wind and moving objects such as leaves causes irregular amplitude fluctuations, and reflections of sound waves from the vegetation result in reverberation (Richards & Wiley 1980). Because reverberation, irregular amplitude fluctuations and frequency-dependent attenuation of a transmitted signal all increase with increasing propagation distance, each provides information that a receiver could use to estimate a singer's distance.

Here I present a study on the importance of two of the different forms of sound degradation for auditory distance assessment in a long range communication system. I tested whether Carolina wrens, *Thryothorus ludovicianus*, can independently use reverberation and high-frequency attenuation of a song to estimate the distance of a singing conspecific. I simulated a singing neighbour by playing its song from inside a subject's territory and predicted that the subject would approach the loudspeaker when clear (unaltered) songs were played, but not when reverberated, high-frequency attenuated, or naturally degraded songs were played. Carolina wrens are excellent subjects for an investigation of auditory distance perception because they usually approach singing intruders silently but counter-sing from a distance if the song comes from further away (Richards 1981). They occupy large territories year-round in diverse habitats, including forests and relatively open areas (Morton & Shalter 1977; Simpson 1982).

## METHODS

### General

I conducted the study at the Mason Farm Biological Reserve in Chapel Hill, North Carolina, in mature oak-hickory forest with shrub undergrowth. Subjects were 12 territorial male Carolina wrens. I estimated territory boundaries by plotting song posts on a detailed map of the study area and by observing the birds on an almost daily basis during the months preceding

the experiments (January–April 1993). A 25-m grid of markers was used to determine territory sizes (ca 150 m in diameter) and distances between singing birds. All subjects had mates, and presumably most of them already had eggs during the beginning of the experiments. Although I did not systematically check territories for fledglings, I observed offspring in territories of two subjects at the end of the experiment.

### Production of Playback Tapes

I selected clear examples of 12 song types from recordings made 3–10 m from singing birds with a Sennheiser K3U/ME88 microphone and a Sony WM-D6C tape-recorder. The songs were chosen after they had been checked for clarity with a real-time spectrum analyser (Kay Electrics DSP Sona-Graph Model 5500). I then sampled the songs at 22050 Hz and 16-bit accuracy on a Macintosh computer with Audiomed software. To standardize the amplitude for re-recording, I adjusted all songs to the same amplitude using the Audiomed software. During re-recording on a Marantz PMD 221 tape-recorder, I kept the recording level the same for all treatments.

I produced tapes of clear songs by re-recording songs through a Krohn-Hite bandpass frequency filter (Model 3700; 1–10 kHz, Butterworth filter function). I produced high-frequency attenuated songs in the same way except with a low-pass setting at 3 kHz, which resulted in attenuation of 24 dB per octave above 3 kHz. This attenuation was similar to propagation over more than 100 m in deciduous forest (Morton 1975; Marten & Marler 1977) and within the range of earlier experiments that: naturally degraded songs (Richards 1981: 50 m; McGregor et al. 1983: 120 m; McGregor & Falls 1984: 200 m; McGregor & Krebs 1984: 100 m). I also chose this relatively intense high-frequency attenuation because isolating one potential cue presents conflicting messages. Because other potential auditory distance cues cannot be completely eliminated in field experiments, I emphasized the cue under investigation.

I produced tapes of naturally degraded songs by broadcasting clear songs through 50 m of deciduous forest and re-recording the songs with a Sennheiser K3U/ME80 microphone on a Marantz PMD 221 tape-recorder. The re-recorded songs were adjusted to the same amplitude as the

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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 × 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/ME80) and loudspeaker (Realistic horn speaker, frequency response 1.5–2.5 kHz ± 3 dB, 2.5–8 kHz ± 2.5 dB) so 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

Playbacks 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 3.5 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 playbacks to 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 playbacks to another subject. At least 2 days lapsed 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 clamped 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-702 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

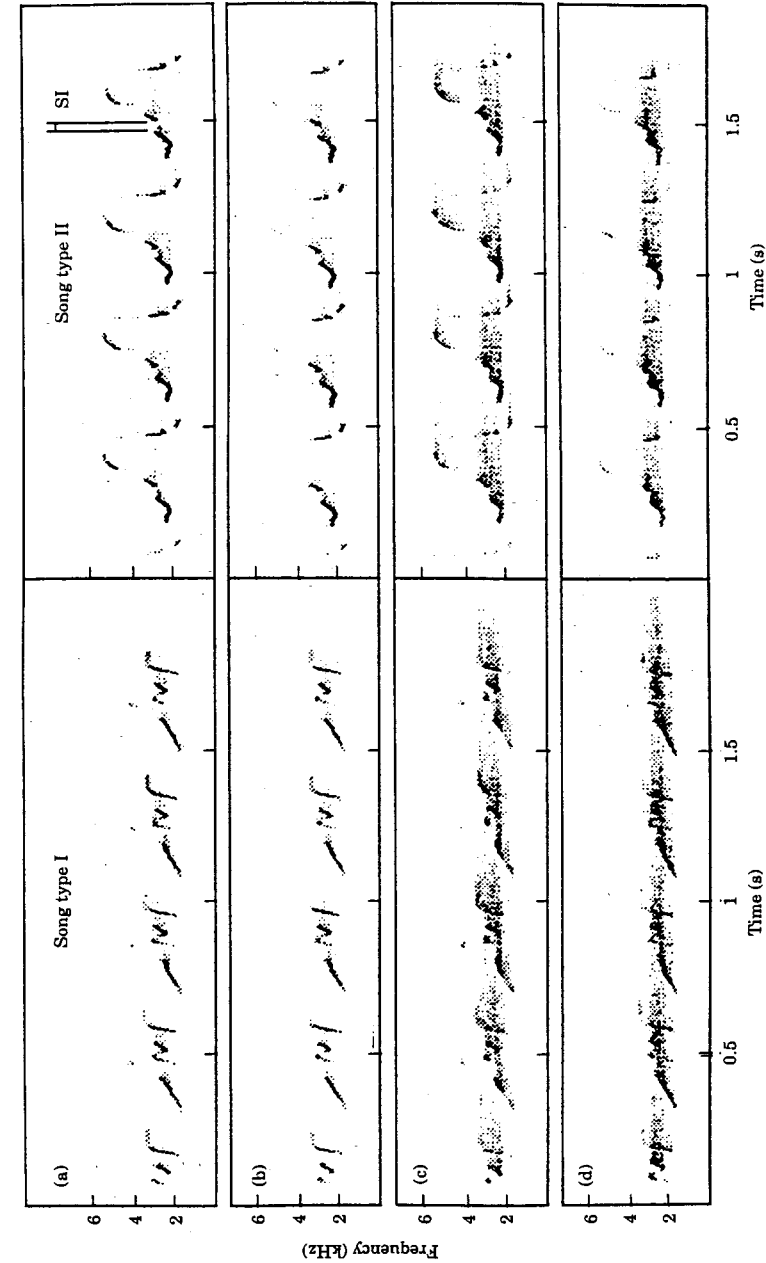


Figure 1. Spectrograms of each treatment of two song types (I, II) used for playback: (a) clear (unaltered) songs, (b) high-frequency attenuated songs, (c) reverberated songs, (d) naturally degraded songs. SI: Shortest silent interval between consecutive elements containing the same frequencies.

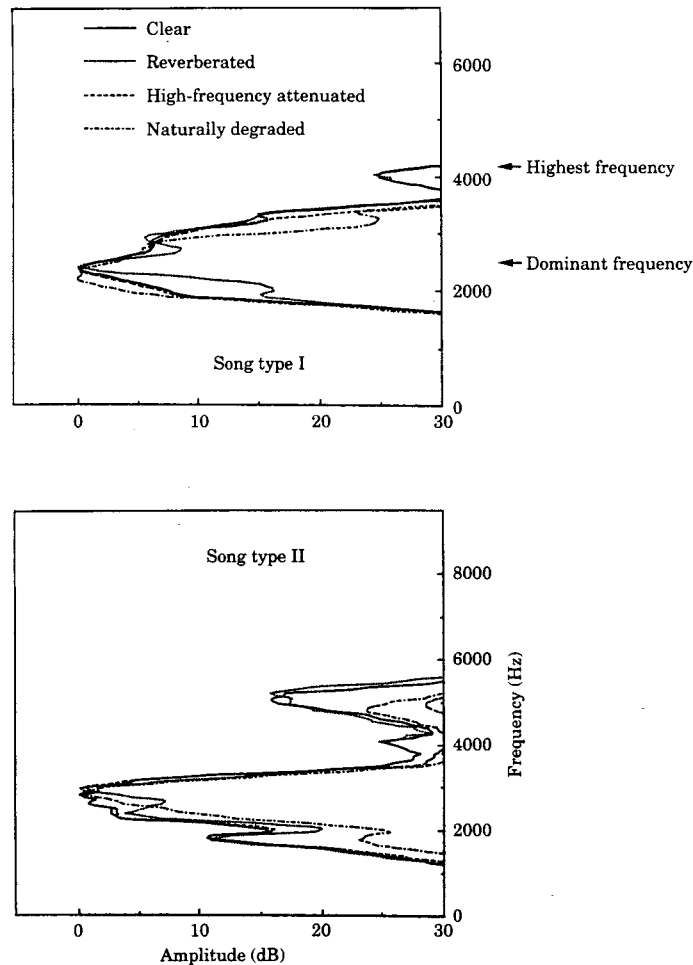


Figure 2. Power spectra of the two song types (I, II) presented in Fig. 1. The peak value (dominant frequency) in each spectrum is set to 0 dB and spectra of the four treatments are overlaid for each song type. Note the absence of the high-frequency peak in high-frequency attenuated and naturally degraded songs.

response measures on vocal responses, which were recorded with a Sennheiser K3U/ME88 directional microphone and a Sony WM-D6C tape-recorder. I extracted the following response measures from the tapes: (1) approach within 25 m of the loudspeaker, (2) latency until the subject resumed singing (the subjects stopped

singing during playback in all except five trials), (3) number of songs within 15 min following the playback, (4) number of songs within 25 m and 30 min following the playback, (5) number of songs in the first bout (a bout terminated when a subject stopped singing for more than 1 min), (6) number of song bouts within 30 min, and (7)

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 analyser, 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.

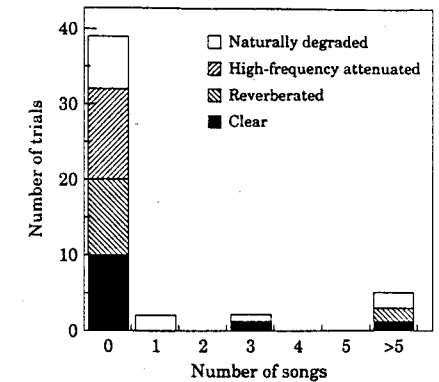


Figure 3. Number of songs that subjects sang after playback began ( $N=47$ ). More than five songs indicated that the subjects sang throughout the playback.

## 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, R: one-tailed  $P=0.023$ ; C, F: one-tailed  $P=0.007$ ; C, D: one-tailed  $P=0.01$ ; R, F: two-tailed  $P=0.705$ ; R, D: two-tailed  $P=0.414$ ; F, D: two-tailed  $P=0.564$ ; 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

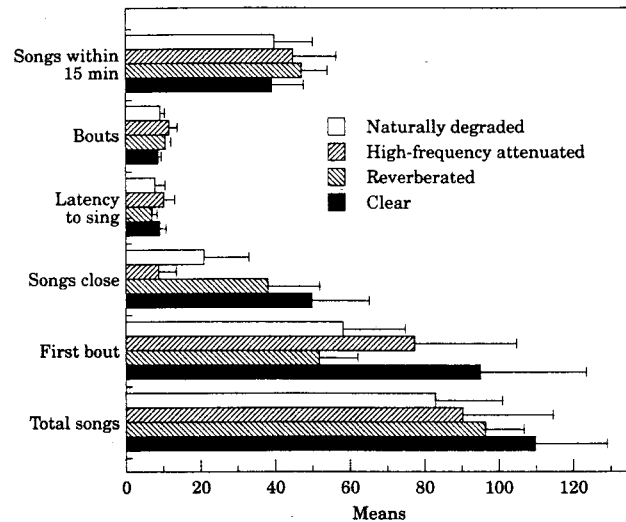


Figure 4. Mean (+SE) vocal responses to the different treatments. Songs within 15 min=number of songs within 15 min following playback; Bouts=number of song bouts (multiplied by 5); Latency to sing=latency until the subject resumed singing; Songs close=number of songs within 25 m; First bout=number of songs in first bout; Total songs=total number of songs.

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  $r=0.06$  to  $0.631$ . 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

Table I. Loadings of the different measures of response on the first (PC1), second (PC2) and third (PC3) principal components

Response measures	Loadings		
	PC1	PC2	PC3
Approach	0.673	0.309	-0.540
Songs in first bout	0.577	0.441	0.527
Songs within 25 m	0.651	0.529	-0.319
Latency to resume singing	0.772	-0.454	0.049
Number of singing bouts	-0.677	0.090	-0.527
Songs within 15 min	-0.541	0.732	0.237

Table II. Analysis of variance of scores on the first principal component of response measures

Source	df	F	P
Treatment	3	3.211	0.045
Song type, individual	11	6.135	0.000
Order	3	0.507	0.682
Treatment*Order	9	0.526	0.839

Table III. Comparison of responses to the different playback treatments as measured by scores on the first principal component of response measures

Treatments	P*	Treatments	P†
C, F	0.002	F, R	0.929
C, R	0.031	F, D	0.695
C, D	0.017	R, D	0.286

C: Clear (unaltered) song; R: reverberated song; F: high-frequency attenuated song; D: naturally degraded song. Wilcoxon matched-pairs signed-ranks test: \*one-tailed, †two-tailed.

( $r=-0.276$ ). Strength of response significantly increased, however, with increasing length of silent intervals between elements that included the same frequencies ( $r=0.472$ ,  $N=47$ ).

#### 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.

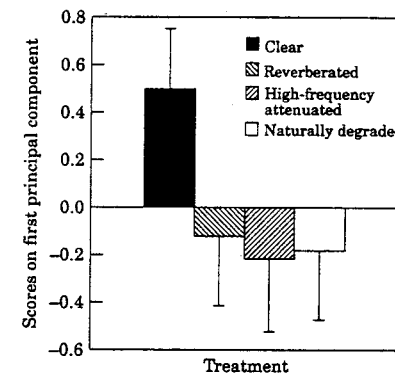


Figure 5. Mean (+SE) scores on the first principal component of responses to each treatment.

no significant differences between the responses to playback of reverberated, high-frequency attenuated and naturally degraded songs (Table III).

The linear regressions showed an increase in response strength with increasing highest and dominant frequencies of song types, but the trends were not significant ( $r=0.234$  and  $r=0.161$ , respectively;  $N=47$ ). There was no significant correlation between these two frequency measures

All prior ranging 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 procedure 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 perceived 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, birds most often hear naturally degraded songs, so they might habituate to them and thus respond weakly when such songs are presented in a playback experiment (Wiley & Wiley 1977; Wiley & Godard, in press). Clear songs, on the other hand, are less frequently heard and might elicit a stronger response during playback. Although habituation to naturally degraded songs could generalize somewhat to any degraded song, the similar responses to clearly differing kinds of degradation in this experiment suggest that habituation did not have a major effect on responses.

These interpretations are supported by recent experiments that further limited subjects' close-range experience with the loudspeaker and where subjects' flights beyond the loudspeaker in response to degraded songs provided unambiguous evidence for ranging (Wiley & Godard, in press; unpublished data).

#### Reverberation

Because any changes in the spectral composition caused by reverberating songs in a large

chamber did not cause high-frequency attenuation, the subjects were not likely to have used spectral cues to assess the distance of the simulated rival when these reverberated songs were broadcast. Instead, the presence of high frequencies with normal intensity in reverberated songs provided conflicting range information and presumably contributed to the high variance in responses.

Reverberation is a reliable distance cue because habitat 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 reverberated '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 did not influence 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 these intervals could indicate that subjects ranged songs differently, dependent on the length of the intervals. If songs in which the same frequencies are repeated at longer intervals elicit a generally stronger response or in fact are ranged differently, a bird might then use such songs to deceive potential receivers by providing less precise information about its location (Morton 1982, 1986; Krebs & Dawkins 1984; Wiley 1994).

Both animals and humans can use reverberation to estimate the auditory distance of a signal. Kentucky warblers, *Oporornis formosus*, misjudged the location of a loudspeaker when reverberated song was broadcast (Wiley & Godard, in press), and howler monkeys, *Alouatta palliata palliata*, regulate their spacing by using reverberation of conspecific calls to estimate the distance to adjacent groups (Whitehead 1987). Humans can also use the reverberation of tone pulses to estimate auditory distance, even if they have had no prior experience with the signals (von Békésy 1938; Mershon & King 1975; Mershon & Bowers 1979). Birds, however, face a less difficult situation

when hearing singing conspecifics, because they presumably already have prior knowledge of species-specific song features (Becker 1982). If so, prior auditory experience with a specific song type may not be necessary to use reverberation as an auditory distance cue (Naguib & Wiley 1994; Wiley & Godard, in press). For instance, knowledge that tonal frequency sweeps are a species-specific characteristic provides enough information to enable a receiver to range such songs by reverberation.

#### High-frequency Attenuation

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 about the distance of a signaller. Also, when territories are established in an open environment, reverberation is negligible. Regardless of habitat and weather conditions, attenuation of a signal disproportionately affects higher frequencies (e.g. Morton 1975; Marten & Marler 1977). Thus, assessing the relative intensities of high frequencies within a song is presumably the most reliable cue in conditions where reverberation and irregular amplitude fluctuations are low, such as in an open environment on a still day. As for ranging by reverberation or degradation in general, however, the accuracy of ranging by frequency-dependent attenuation requires further investigation.

To use frequency-dependent attenuation to range a song, a receiver has to compare the frequency characteristics of a received song with those at the source. From such a comparison the receiver could then estimate the length of the propagation path and thus the distance of the singer. However, Carolina wrens have large song repertoires and might occasionally need to range song types that they have not heard frequently. Here, ranging by spectral cues alone could become less accurate because song types vary considerably in maximal and dominant frequencies (Borror 1956; unpublished data). In this case the situation resembles that for humans, who use the high-frequency content of an unknown signal as a cue for auditory distance only after repeated presen-

tations or as a relative cue compared to the perceived distance of a known signal (Coleman 1962, 1968; Little et al. 1992). These considerations suggest that familiarity with a song could have a stronger influence on the accuracy of ranging by birds, when the relative intensities of high frequencies provide the only auditory distance cue than when reverberation provides the only cue.

Song birds might also be able to estimate auditory distance in a relative manner when they cannot judge the absolute distance of a singer. This common issue in human psychology (Mershon & Bowers 1979; Little et al. 1992) has not yet been addressed in studies of animal communication. All potential auditory distance cues, including the overall amplitude (Naguib 1995), might then be used to range the position of a conspecific in relation to other singing birds or in comparison to prior songs of that individual.

In summary, the use of reverberation and the relative intensities of high frequencies as auditory distance cues suggest that Carolina wrens' ranging abilities are adapted to the varying acoustic properties of their environment. In addition, pooling information acquired from different physical characteristics of a song is likely to increase the accuracy of ranging.

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#### REFERENCES

- Becker, H. P. 1982. The coding of species-specific characteristics in bird sounds. In: *Acoustic Communication in Birds, Vol. 1* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 213–252. New York: Academic Press.
- von Békésy, G. 1938. Über die Entfernungsempfindung beim Hören. *Akust. Z.*, 3, 21–31.

- Borror, D. J. 1956. Variation in Carolina wren songs. *Auk*, **73**, 211–229.
- Brindley, E. L. 1991. Response of European robins to playback of song: neighbour recognition and overlapping. *Anim. Behav.*, **41**, 503–512.
- Coleman, P. D. 1962. Failure to localize the source distance of an unfamiliar sound. *J. acoust. Soc. Am.*, **34**, 345–346.
- Coleman, P. D. 1968. Dual role of frequency spectrum in determination of auditory distance. *J. acoust. Soc. Am.*, **44**, 631–632.
- Krebs, J. R., Ashcroft, R. & Webber, M. 1978. Song repertoires and territory defense in the great tit. *Nature, Lond.*, **271**, 539–542.
- Krebs, J. R. & Dawkins, R. 1984. Animal signals: mind reading and manipulation. In: *Behavioural Ecology: An Evolutionary Approach*. 2nd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 380–402. Oxford: Blackwell Scientific Publications.
- Kroodsma, D. E. & Byers, E. B. 1991. The function(s) of bird song. *Am. Zool.*, **31**, 318–328.
- Little, A. D., Mershon, D. H. & Cox, P. H. 1992. Spectral content as a cue to perceived auditory distance. *Perception*, **21**, 405–416.
- McGregor, P. K. 1992. Quantifying responses to playback: one, many or multivariate composite measures? In: *Playback Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 79–96. New York: Plenum Press.
- McGregor, P. K. & Falls, J. B. 1984. The response of western meadowlarks (*Sturnella neglecta*) to the playback of degraded and undegraded songs. *Can. J. Zool.*, **62**, 2125–2128.
- McGregor, P. K. & Krebs, J. R. 1984. Sound degradation as a distance cue in great tit (*Parus major*) song. *Behav. Ecol. Sociobiol.*, **16**, 49–56.
- McGregor, P. K., Krebs, J. R. & Ratcliffe, L. M. 1983. The reaction of great tits (*Parus major*) to playback of degraded and undegraded songs: the effect of familiarity with the stimulus song type. *Auk*, **100**, 898–906.
- Marten, K. & Marler, P. 1977. Sound transmission and its significance for animal vocalizations. I. Temperate habitats. *Behav. Ecol. Sociobiol.*, **2**, 271–290.
- Mershon, D. H. & Bowers, J. N. 1979. Absolute and relative cues for the auditory perception of egocentric distance. *Perception*, **8**, 311–322.
- Mershon, D. H. & King, L. E. 1975. Intensity and reverberation as factors in the auditory perception of egocentric distance. *Percept. Psychophys.*, **18**, 409–415.
- Michelsen, A. 1978. Sound reception in different environments. In: *Sensory Ecology* (Ed. by M. A. Ali), pp. 345–373. New York: Plenum Press.
- Morton, E. S. 1975. Ecological sources of selection on avian sounds. *Am. Nat.*, **109**, 17–34.
- Morton, E. S. 1982. Grading, discreteness, redundancy, and motivation-structural rules. In: *Acoustic Communication in Birds, Vol. 1* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 183–212. New York: Academic Press.
- Morton, E. S. 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. *Behaviour*, **99**, 65–86.
- Morton, E. S. & Shalter, M. D. 1977. Vocal response to predators in pair-bonded Carolina wrens. *Condor*, **79**, 222–227.
- Naguib, M. 1995. Perception of auditory distance in song birds and its implications for long-range communication. Ph.D. thesis, University of North Carolina, Chapel Hill.
- Naguib, M. & Wiley, R. H. 1994. Perception of auditory distance in song birds: how much prior information does a listener need? *J. Ornithol.*, **135**, 167.
- Piercy, J. E., Embelton, T. F. W. & Sutherland, L. C. 1977. Review of noise propagation in the atmosphere. *J. acoust. Soc. Am.*, **61**, 1403–1418.
- Richards, D. G. 1981. Estimation of distance of singing conspecifics by the Carolina wren. *Auk*, **98**, 127–133.
- Richards, D. G. & Wiley, R. H. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Am. Nat.*, **115**, 381–399.
- Shy, E. & Morton, E. S. 1986. The role of distance, familiarity, and time of day in Carolina wrens responses to conspecific songs. *Behav. Ecol. Sociobiol.*, **19**, 393–400.
- Simpson, B. S. 1982. Communication with complex vocal repertoires by a territorial passerine, the Carolina wren. Ph.D. thesis, University of North Carolina, Chapel Hill.
- Sokal, R. R. & Rohlf, F. J. 1987. *Introduction to Biostatistics*. 2nd edn. New York: W. H. Freeman.
- Whitehead, J. M. 1987. Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys, *Alouatta palliata palliata*. *Anim. Behav.*, **35**, 1615–1627.
- Wiley, R. H. 1994. Errors, exaggeration and deception in animal communication. In: *Behavioral Mechanisms in Ecology* (Ed. by L. Real), pp. 157–189. Chicago: University of Chicago Press.
- Wiley, R. H. & Godard, R. In press. Ranging of conspecific songs by Kentucky warblers and its implications for interactions of territorial males. *Behaviour*.
- Wiley, R. H. & Richards, D. G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.*, **3**, 69–94.
- Wiley, R. H. & Richards, D. G. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic Communication in Birds, Vol. 2* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 131–181. New York: Academic Press.
- Wiley, R. H. & Wiley, M. S. 1977. Recognition of neighbors' duets by stripe-backed wrens *Campylorhynchus nuchalis*. *Behaviour*, **62**, 10–34.