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Ranging of songs with the song type on use of different cues in Carolina wrens: effects of familiarity

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Abstract Male territorial song birds are usually spaced far apart and most often hear conspecific song after it has been degraded by propagation through the environment. Their ability to use the degradation of songs to assess the distance of a singing rival without approaching (called ranging) presumably increases the efficiency of defending a territory. In order to assess degradation in a song the receiver needs to compare the characteristics of the received song to its characteristics at the source or at different distances. Earlier experiments on ranging in species with song repertoires have suggested that prior familiarity with the particular song type is necessary for ranging. Here I show that male Carolina wrens (*Thryothorus ludovicianus*) can use either temporal or spectral characteristics for ranging song types which they were unlikely to have heard previously. Playbacks consisting of only one song prevented subjects' close-range experience with the loudspeaker, and flights beyond the loudspeaker provided direct evidence for over-assessment of distance when songs were degraded. Because ranging of songs was not affected by the degree of familiarity with the song type, this experiment provides no evidence that song repertoires hinder ranging in Carolina wrens, as suggested by Morton's ranging hypothesis. Instead, at least approximate ranging of songs is evidently possible by assessment of degradation in general features of a species' songs.

Key words Bird song · Carolina wren · Environmental acoustics · Distance perception · Song repertoires

Introduction

Several studies have shown that male territorial song birds can use auditory cues to assess the distance of singing conspecifics (called ranging) (Richards 1981; McGregor et al. 1983; McGregor and Falls 1984; McGregor and Krebs 1984; Shy and Morton 1986; Brindley 1991; Naguib 1995b, 1996a, 1997; Wiley and Godard 1996; Morton and Derrickson 1996; Fotheringham et al. 1997; but see Fotheringham and Ratcliffe 1995). Ranging is thought to be an adaptation for efficiently defending a territory or in general to regulate spacing. Cues for ranging are provided by the accumulating degradation of songs during propagation through the environment (Michelsen 1978; Wiley and Richards 1978, 1982), such as by reverberation and frequency-dependent attenuation (Naguib 1995b) or by changes in song amplitude (Naguib 1997). The ability to use these cues for ranging requires that a receiver compares the characteristics of the received (degraded) song to its characteristics at its source or at different distances. By such a comparison a receiver then could assess the degree of degradation and, along with some experience with the acoustics of its habitat (Naguib 1996a), estimate the propagation distance, and therefore the distance of the singer. It has remained controversial how much prior information about a song a receiver requires in order to assess its degree of degradation. This question, however, is crucial not only for understanding the mechanisms receivers might use to extract information from a song about auditory distance but also for understanding the role of ranging in interactions among conspecific males.

Morton's ranging hypothesis suggests that ranging a song requires production of the particular song type (Morton 1982, 1986, 1996). Experiments, however, indicated that auditory experience with the song type is sufficient for ranging. Great tits (*Parus major*) (McGregor and Krebs 1984) and western meadowlarks (*Sturnella neglecta*) (McGregor and Falls 1984) discriminated between playback of undegraded and de-

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graded songs which they did not sing themselves only when they had had prior auditory experience with the particular song type. In other experiments, responses of great tits suggested that they discriminated among unfamiliar undegraded and degraded songs, but only when they were similar to song types known to the subjects (McGregor et al. 1983). Kentucky warblers (*Oporornis formosus*), however, ranged unknown songs without regard to the songs' similarities to ones with which they had had frequent experience (Wiley and Godard 1996). Although it is reasonable to assume that for ranging a receiver needs to have some prior information about the structure of the signal at its source, the experiments taken together do not provide a clear picture of the nature of this information.

Morton (1982, 1986) further suggested that an inability to range songs not in the receiver's own vocal repertoire would influence the evolution of large song repertoires in Carolina wrens and possibly other species. Individuals that could sing unfamiliar ("unrangeable") songs could disrupt receivers' behavior, resulting in a relative increase in the sender's fitness. Although these arguments have not been supported by the experiments mentioned above, they have not been tested yet on species with large song repertoires. In addition, it has been proposed that individuals interact by matched counter-signing (two individuals singing the same song pattern) in order to provide the recipient with accurate information on location (Krebs et al. 1981; McGregor and Falls 1984; McGregor 1991). This hypothesis, however, hinges on whether or not shared songs can be ranged more accurately than unshared songs.

The contrasting results and divergent interpretations of ranging experiments might arise in part because songs were degraded in different ways in the different experiments. The studies on western meadowlarks (McGregor and Falls 1984) and great tits (McGregor et al. 1983; McGregor and Krebs 1984), for instance, degraded songs by broadcasting them in the subjects' open or semi-open habitats, so that the songs were presumably degraded primarily by frequency-dependent attenuation and irregular amplitude fluctuations (Richards and Wiley 1980; Wiley and Richards 1982). In contrast, songs in the study with Kentucky warblers (Wiley and Godard 1996) were degraded only by reverberation. Although male Carolina wrens can use either the relative intensities of high frequencies or reverberation of a song to range conspecifics (Naguib 1995b), these findings were obtained with song types frequently heard by the subjects. However, because all songs in Carolina wrens contain tonal frequency sweeps, assessment of the degree of reverberation is potentially possible for all song types. On the other hand, some song types differ considerably in their spectral composition so that accurate ranging might be problematic when unfamiliar songs are degraded primarily by high-frequency attenuation.

This study investigated the influence of familiarity with song types on the use of either reverberation or high-frequency attenuation as cues for ranging in Caro-

lina wrens. Each playback presented only one song to a subject in order to eliminate the possibility of subjects approaching the loudspeaker during presentation of the stimulus. Subjects that approach a loudspeaker during playback must have ranged the source of broadcast songs correctly so that any subsequent responses could only be used as indirect evidence, if at all, for ranging. The playback of one song also prevented subjects from obtaining information successively during approach about the position of the loudspeaker. The behavior following playback, therefore, was more likely to provide direct evidence for ranging (Naguib 1996a, b).

Methods

General

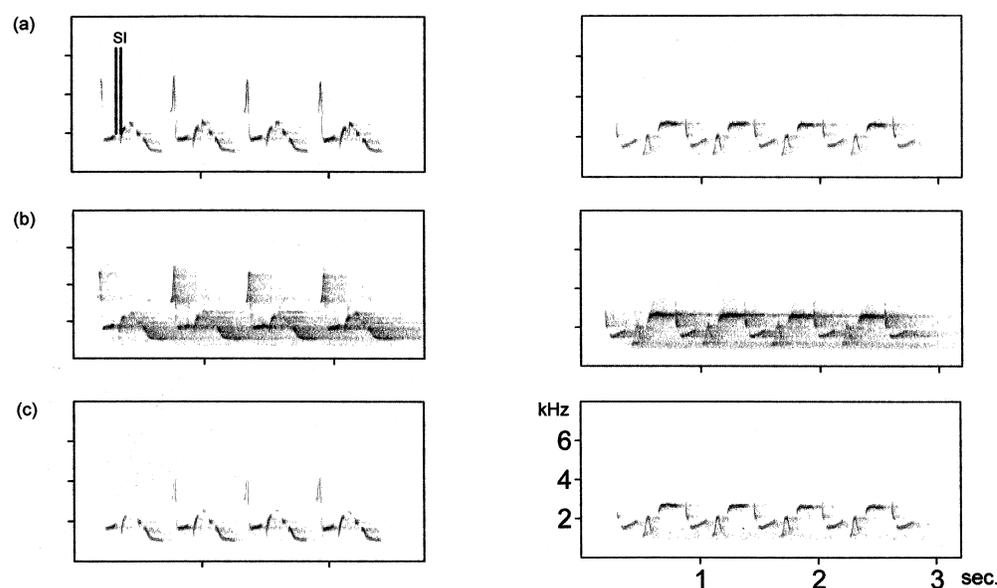
The study of male territorial Carolina wrens was conducted at the Mason Farm Biological Reserve in Chapel Hill, North Carolina, United States, from 26 March until 18 April 1994. Carolina wrens in this area are territorial residents throughout the year, and usually males and females remain paired on their territories throughout one or more breeding seasons. Thus, territories not only serve as a space for breeding but they also are an important food source during winter when birds without territories have reduced probabilities of survival (Morton 1982; Simpson 1984).

For playback experiments 19 males served as subjects, of which 12 received playbacks of songs not recorded in this population (unfamiliar songs) and 7 received playback of songs with which they had had prior close-range experience (familiar songs). Each subject received three different playbacks: undegraded (unaltered), reverberated, and high-frequency attenuated song (Fig. 1). Previous experiments have shown that Carolina wrens can use both kinds of cues for ranging (Naguib 1995b). In this experiment, I examined whether or not familiarity with the song type influenced use of these cues differently. The subjects' territorial boundaries were determined prior to the experiments by plotting their movements and song posts on a detailed map of the study area. A 25-m grid of markers throughout the study area was used to determine territory sizes (about 150 m in diameter) and distances of singing birds. The subjects had started building nests at the beginning of the experiment but no fledglings were observed before the end of the experiment.

Selection of songs

All except two song types were recorded with a Sennheiser ME88/K3U directional microphone and a Sony WM-D6C tape recorder within 3–10 m of singing males. Two song types used as unfamiliar songs were recorded with a Sony parabolic reflector PBR-330 and a Realistic omni-directional dynamic microphone 33-1070A on a Sony TC-D5 Pro II cassette recorder. All songs were then checked for clarity on a real-time spectrum analyzer (Kay Electric's DSP Sona-Graph Model 5500). Familiar songs (in total four song types) were recorded from the subjects' neighbors in order to assure that the subjects had had recent close-range experience with the particular version of the respective song type. Two song types recorded 15 km away from the study area and three song types recorded about 300 km away (Ocracoke, Outer banks, North Carolina) were used as unfamiliar songs. These song types had not been heard during almost daily visits at the study area during the preceding eighteen months. In a comparison to sonograms of over 50 song types recorded in the study area, these song types could clearly be recognized as different. With an average repertoire size of 28 song types (Simpson 1985) and 70–95% sharing of song types between neighbors (Simpson 1985; Shy and Morton 1986), these 50 songs

Fig. 1 Spectrograms of two song patterns with different frequency ranges: **a** undegraded, **b** reverberated, **c** high-frequency attenuated (*SI* silent interval)



used for comparison most likely included all song types present in the study area. These experiments thus employed four familiar and five song types which subjects were unlikely to have heard previously (unfamiliar song types).

Production of playback tapes

All songs were digitized at 20500 Hz with 16-bit accuracy with Audiomeia sound card and Sound Designer II software on a Macintosh II computer. Undegraded (unaltered) songs were produced by re-recording them through a Krohn-Hite band-pass frequency-filter (Model 3700, 1–10 kHz, Butterworth filter function, roll-off 24 dB/octave) on a Marantz PMD221 tape recorder. The high-frequency attenuated songs were produced in the same way except with frequency-filter settings from 1 to 3 kHz. The reverberated songs were produced by playing back the undegraded songs through a Perma Power S-702 amplifier and a Realistic Horn speaker (frequency response, 2–8 kHz, ± 3 dB) in a large attic and re-recording them with a Sennheiser ME80/K3U microphone on a PMD221 tape recorder at a distance of 6 m. The resulting reverberation time was similar to that of songs transmitted through 50 m of deciduous forest, and songs only showed minor changes in spectrum (Naguib 1995a). The attic was chosen over electronic reverberation because its multiple reflecting surfaces created a complex and more natural reverberation than an electronic device. The spectra of reverberated songs were checked prior to playback to make sure that this procedure did not attenuate high frequencies. All songs were re-recorded with the same VU-meter level on the tape recorder.

Playback experiments

The playbacks were conducted from 0600 to 1100 hours to reduce possible effects of time of day (Shy and Morton 1986). Each of the nine song types was presented to two subjects except two of the unfamiliar song types which were presented to three subjects, and one familiar song type which was presented to only one subject as another intended subject had left its territory before the experiment began. Each subject received the three playback treatments at least two days apart in a balanced design. The treatment presented was determined by the roll of a die after the equipment had been set up, subject to the constraint of balancing the order of treatments among individuals.

Each playback consisted of only one song played at a distance of about 30 m from a singing subject but at least 25 m within its

territory. Playbacks were conducted using a Marantz PMD221 tape recorder connected to a Perma Power S-702 amplifier and a Realistic horn loudspeaker (see above) clamped on a small tree about 1.8 m above ground.

The amplifier gain was adjusted to broadcast all songs at an intensity of 88 dB at 1 m distance, as measured with a Realistic sound-level meter (C-weighting, fast response) in a large field with low vegetation, a nearly anechoic environment. This volume was within the range of singing Carolina wrens but lower than the maximum level of 110 dB reported by Morton (1982) for Carolina wrens. Song broadcast at maximum volume in any case would indicate a nearby rival and thus would confound tests on use of separate cues for ranging.

Response measures

I predicted on the basis of prior experiments that only those subjects that assessed the correct location would approach the loudspeaker. Subjects that assessed the song as coming from within their territory but from a more distant location would move beyond the loudspeaker, and those subjects that assessed the song as coming from beyond the territorial boundary would not approach. Thus I distinguished between approach (within 20 m of the loudspeaker but not past it), approach to a position beyond the loudspeaker, and no observed approach. I only scored movements as approach when subjects approached within 20 m of the loudspeaker, because smaller movements towards the loudspeaker could not be detected reliably in all cases. Thus, approach within the range of 20 m of the loudspeaker was used as an indicator of subjects having assessed the source of the song as being inside the territory. Additional response measures were total number of songs, number of songs in the longest singing bout, number of songs beyond the loudspeaker, percentage of songs beyond the loudspeaker, time spent beyond the loudspeaker, distance the loudspeaker was over-flown, and approach distance (closest approach measured from the loudspeaker in the subjects' original direction for those subjects that did not fly beyond the loudspeaker and the farthest distance subjects moved away from the loudspeaker on its far side for those that over-flew the loudspeaker). High values for the first two measures of response indicated a generally intense response whereas high values for the latter five measures indicated more directly that subjects over-estimated the position of the loudspeaker. In order to assess if consistent differences in latencies to respond to the different playback treatments would confound other measures of response I measured latencies of

subjects to approach and their latencies to move beyond the loudspeaker. However, I did not include these posthoc measures in the statistical analysis, in part because these measures were not available for trials in which subjects did not approach. Overall, I recorded responses for 45 min after playback stopped. I chose such a comparatively long period for recording data as earlier experiments had shown that Carolina wrens often perched silently after initial approach and then started to respond vigorously after long latencies. In addition, preliminary and earlier experiments (Naguib 1995b, 1996a) with only one song had shown that subjects responded for a longer time compared to playbacks of longer duration, presumably because they were more uncertain where the simulated rival remained. In addition, strangers rarely appear in spring as young birds establish territories in summer and fall, and most birds without territories appear to have reduced chances of survival (Morton 1982; Simpson 1984). Thus, intrusions might be perceived as particularly severe in such a relatively stable territorial system.

Statistical analysis

The primary measure of response, approach, was first analyzed separately with *G*-tests. Because the response measures correlated with each other ($r = 0.049$ to 0.834), for further analysis I used a principal component analysis to extract one composite measure of response for each playback. The first principal component which explained 47% of the variance in response, was then used as an overall measure of response in further analyses. The second component explained an additional 24% of variance. Response measures and their respective loadings on the first principal component were: (1) total number of songs (-0.214), (2) number of songs in longest singing bout (-0.275), (3) number of songs beyond the loudspeaker (0.880), (4) percentage of total songs beyond the loudspeaker (0.885), (5) time spent beyond the loudspeaker (0.927), (6) distance that subjects moved away from the loudspeaker on its far side (0.898), (7) approach distance (0.574), and (8) approach category (0.245). I here also included the approach categories mentioned above because of the possibility that the two contrasting responses to distant sounding songs in Carolina wrens (no approach vs. flights to positions beyond the loudspeaker; Richards 1981, Naguib 1996a) concealed each other in the analysis. Approaches were scored as follows: (1) approach within 20 m of the loudspeaker (scored as 1); (2) movement beyond the loudspeaker (scored as 2), the expected behavior for subjects that over-estimated the position of the loudspeaker within the range of territory; and (3) no close approach or movements beyond the loudspeaker (scored as 3), the expected response for subjects that ranged the song as coming from beyond the territorial boundary.

Because of these two contrasting kinds of reactions to degraded songs (no approach or movements beyond the loudspeaker), differences in responses to playback of degraded and undegraded songs could be concealed by pooling the data, as mentioned above. In addition, although "no approach" is the expected response for subjects estimating the song as coming from beyond the boundary, confounding factors can not be ruled out as clearly as when subjects approached to positions beyond the loudspeaker (Naguib 1996a; Wiley and Godard 1996). Thus, in a second analysis, I eliminated all trials in which subjects were not observed moving towards the loudspeaker. This analysis then was restricted to those trials in which subjects showed unambiguous responses by either closely approaching or moving beyond the loudspeaker. Eliminating trials with no approach reduced the potential influence of factors other than ranging on responses and also made it unnecessary to categorize the approach. The first principal component extracted from this reduced data set (42 out of 57 playbacks) explained 57% of the variance in responses and the second component explained an additional variance of 24%. The loadings of the response measures on the first principal component were: (1) total number of songs (-0.238), (2) number of songs in longest singing bout (-0.311), (3) number of songs beyond the loudspeaker (0.872), (4) percentage of total songs beyond the loudspeaker (0.878),

(5) time spent beyond the loudspeaker (0.933), (6) distance that subjects moved away from the loudspeaker on its far side (0.914), and (7) approach distance (0.772).

Frequency-dependent attenuation might be more difficult to assess in songs with little initial energy in high frequencies. Thus, it is possible that the frequency composition of songs affects the accuracy with which receivers can assess frequency-dependent attenuation. Because response intensities in an earlier experiment were affected by the songs' frequency characteristics (Naguib 1995b), I measured highest and dominant frequency of songs to test further if such song parameters influence ranging. In addition it is possible that birds might use the length of silent intervals between elements with similar frequencies as a standard to assess reverberation, as suggested by Wiley and Godard (1996). This parameter also correlated with intensity of responses in an earlier experiment on ranging in Carolina wrens (Naguib 1995b). Thus, to test if reverberation can be assessed more accurately in songs with particular temporal structures, I measured the minimal intervals between elements with similar frequencies on sonograms (Avisoft Pro, R. Specht, Berlin) (Fig. 1).

Results

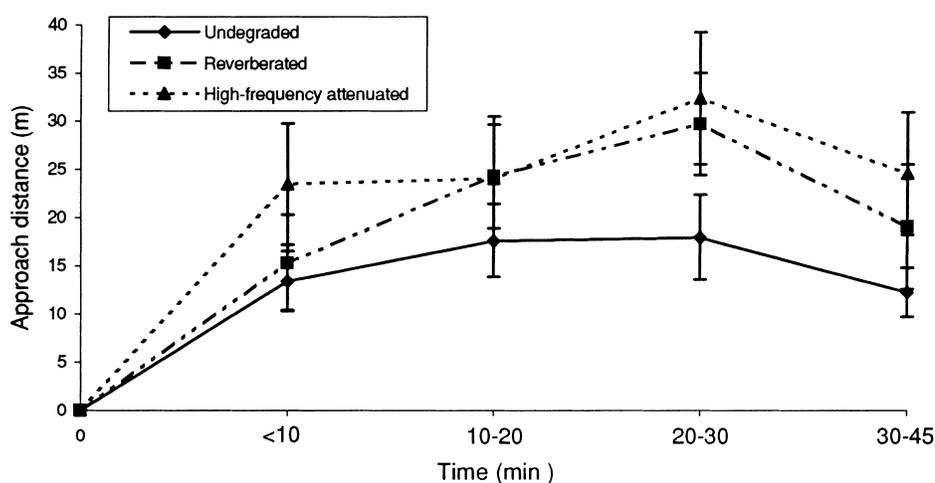
Approach and other response measures

Most subjects approached the loudspeaker in response to undegraded songs whereas most subjects over-flew it or did not approach in response to the two kinds of degraded songs. The approaches differed significantly among playback treatments ($P < 0.005$, $df = 4$, *G*-test) but did not indicate that the subjects' auditory distance assessment was influenced by prior experience with the song type (number of subjects that moved to the three different locations: undegraded songs, 15 close (6+9), 4 beyond (1+3), 0 no approach; reverberated songs, 2 close (1+1), 11 beyond (4+7), 5 no approach (1+4); high-frequency attenuated songs, 2 close (1+1), 8 beyond (2+6), 8 no approach (3+5)) (numbers in parentheses refer to playbacks of familiar and unfamiliar songs, respectively). These differences in approach were apparent throughout the time in which responses were recorded (Fig. 2).

In general, subjects responded more intensely to undegraded than to reverberated and high-frequency attenuated songs. Subjects sang more songs and longer singing bouts in response to playback of undegraded songs than in response to playback of degraded songs (Fig. 3a, b). In contrast, differences in response beyond the loudspeaker were reversed. Here subjects responded more intensely to the two kinds of degraded songs compared to undegraded songs and responses beyond the loudspeaker tended to be strongest after playback of high-frequency attenuated songs (Fig. 3a, b). These latter responses directly indicated an over-estimation of the distance of the loudspeaker when reverberated and high-frequency attenuated songs were played.

The responses did not indicate any consistent difference between playback of familiar and unfamiliar songs, regardless of whether they were high-frequency attenuated or reverberated (cf. Fig. 3a, b).

Fig. 2 Mean approach distance (\pm SE) of subjects in different time segments in which responses were recorded. Approach distance is shown as total distance moved away from the subjects' original position towards and if applicable beyond the loudspeaker



Principal component scores

The playback treatment had a significant influence on overall responses measured by the scores on the first principal component in an analysis of variance. There was no significant influence of familiarity with the song type, or of the interaction between treatment and familiarity (playback treatment, $F_{2,51} = 3.543$, $P = 0.037$; familiarity with the song type, $F_{1,51} = 0.116$, $P = 0.735$; interaction between treatment and familiarity, $F_{2,51} = 0.158$, $P = 0.855$) (Fig. 4). These results remained when cases in which subjects did not approach were excluded (playback treatment, $F_{2,39} = 4.568$, $P = 0.017$; familiarity with the song type, $F_{1,39} = 0.194$, $P = 0.663$; interaction between treatment and familiarity, $F_{2,39} = 0.063$, $P = 0.939$).

Pair-wise comparisons of the first principal component scores (based on the full data set) showed significant differences between undegraded and both reverberated songs and high-frequency attenuated songs (Table 1). Responses to familiar and unfamiliar song types did not differ in comparisons for any treatment (undegraded, $P = 0.642$; reverberated, $P = 0.735$; high-frequency attenuated, $P = 0.310$; Mann-Whitney U -test, two-tailed). The variation in response was least for undegraded familiar songs (Fig. 4).

In summary, the principal component scores indicated that subjects over-estimated the position of the loudspeaker when songs were degraded regardless of

whether or not they had had prior experience with the song type.

A linear regression of the first principal component scores on the highest and dominant frequencies and the lengths of shortest silent intervals between similar elements did not indicate that these characteristics influenced responses ($r_s < 0.03$, $n = 56$, for regressions on all three song features).

Discussion

General

The results support prior findings that Carolina wrens can use either reverberation or the relative intensities of high frequencies in a song to assess the distance of conspecific singers (Naguib 1995b). In particular subjects' movements to positions beyond the loudspeaker and subsequent strong responses on its far side after playback of reverberated and high-frequency attenuated songs indicated that these cues were sufficient for ranging, at least approximately, even of songs types which they were unlikely to have heard previously. Because the short playback period reduced confounding factors, such as habituation, recognition, and detection (for detailed discussion see Naguib 1996a, b; Wiley and Godard 1996), differences in responses after playback of undegraded and degraded songs appear to be best explained by differences in the estimated distance of simulated rivals.

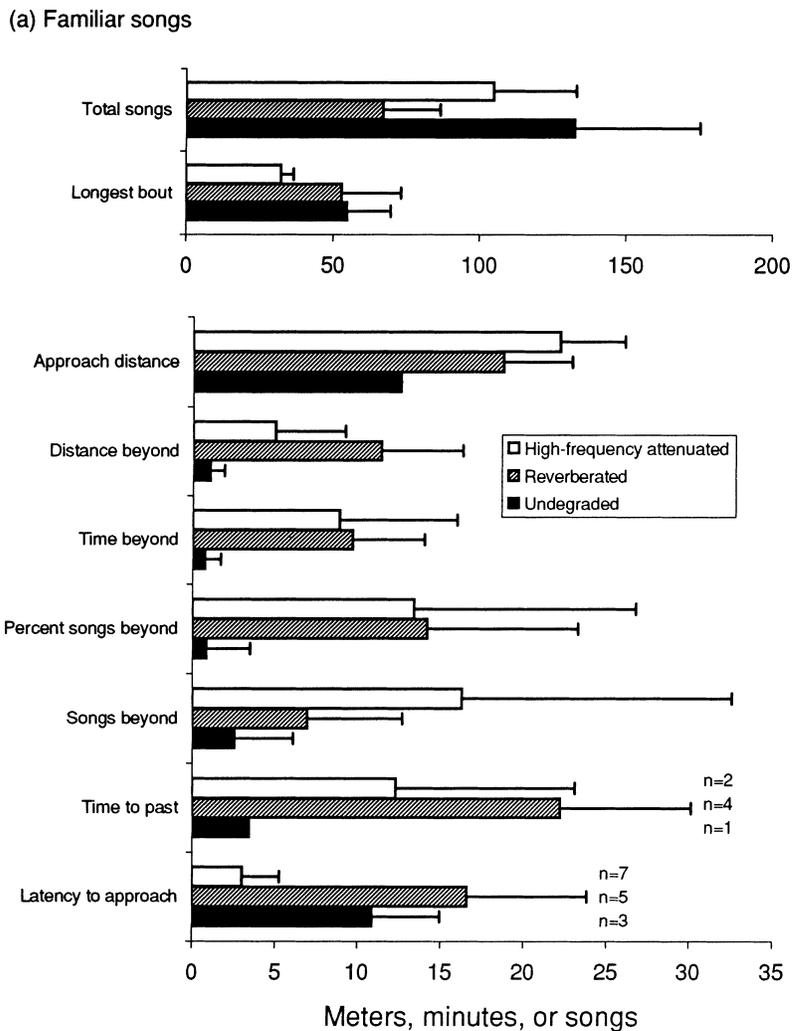
How much prior information about the song is necessary for ranging?

Earlier studies on great tits and western meadowlarks (McGregor and Falls 1984; McGregor and Krebs 1984) found discrimination between degraded and undegraded songs only when subjects were familiar with the song

Table 1 Pairwise comparisons between scores on the first principal component separated by treatment and familiarity. P values are one-tailed, except for R vs. FA comparisons (two-tailed). Wilcoxon matched-pairs signed-rank test (UD undegraded, R reverberated, FA, high-frequency attenuated)

Comparisons	Familiar ($n = 7$)	Unfamiliar ($n = 12$)	All ($n = 19$)
UD vs. R	0.023	0.014	0.002
UD vs. FA	0.023	0.017	0.002
R vs. FA	0.46	0.31	0.88

Fig. 3 Response measures in playbacks with **a** familiar songs ($n = 7$) and **b** unfamiliar songs ($n = 12$)



type. However, Carolina wrens in this experiment, as well as Kentucky warblers (Wiley and Godard 1996),

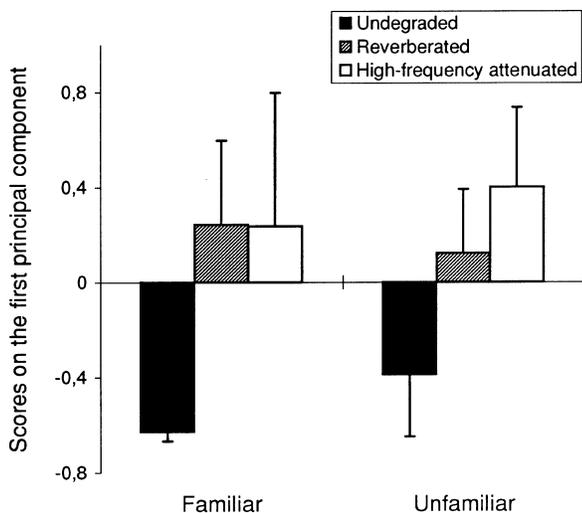


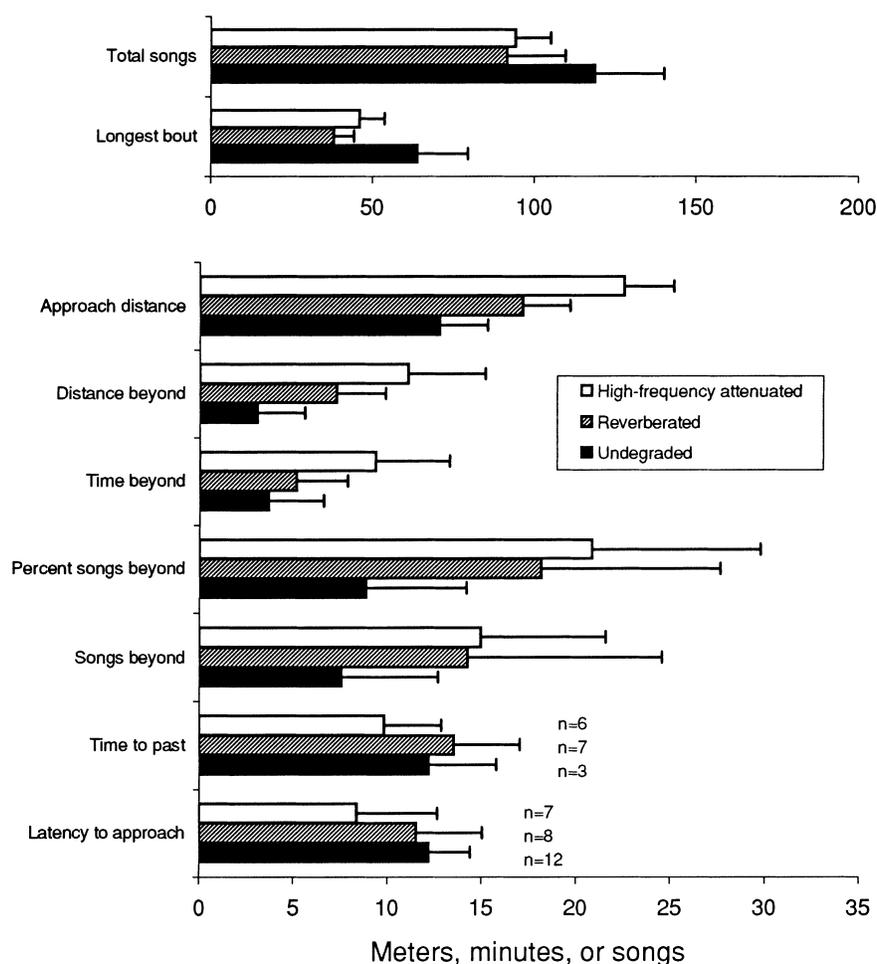
Fig. 4 Mean scores (\pm SE) on the first principal component separated by familiarity with the song type and treatments

ranged song types which they were unlikely to have heard previously. Recently, Morton and Derrickson (1996) also concluded from their study on dusky antbirds (*Cercomacra tyrannina*) that ranging does not require familiarity with the song type.

Morton (1982) stimulated these experiments by suggesting that birds must produce a song pattern in order to use it as an undegraded standard for assessing degradation in a received song. Findings that ranging does not necessarily require prior familiarity with the song type, however, suggest that birds are able to rely on more general song features in order to assess signal degradation. All Carolina wrens' songs, in fact most birds' songs, contain tonal frequency sweeps (Nowicki and Marler 1988), which would allow a listener to assess the degree of reverberation. Therefore, it does not seem surprising that Carolina wrens or Kentucky warblers can range unfamiliar song types by reverberation. Use of such general temporal features in songs to assess degradation that do not require prior experience with a particular song also is in line with earlier findings that Carolina wrens discriminate between undegraded and degraded songs before they develop adult song (Morton

Fig. 3b

(b) Unfamiliar songs



et al. 1986) and can explain approximate ranging of unfamiliar songs by reverberation.

Information on species-specific song features could also allow ranging by the relative intensities of high frequencies when songs are degraded primarily in their spectral composition. In species in which all song types have a similar frequency composition, ranging unfamiliar song types on the basis of the relative intensities of high frequencies might not pose a problem. On the other hand, in species like Carolina wrens, in which song types differ considerably in their spectral characteristics, ranging on the basis of the relative intensities of high frequencies could require more specific information about the song type (Naguib 1995b). The results obtained here, however, do not support this possibility. If high frequencies are attenuated drastically, as in this experiment, or when a song has travelled over a long distance, a comparison to any known song type could enable a listener to assess the approximate distance to the source. For finer discrimination of distance, however, it could be difficult to use spectral characteristics of unknown songs when song types differ widely in their frequency composition. If the low variation in response

to familiar undegraded songs was caused by a higher consistency in the accuracy of subjects' assessment of the position of the loudspeaker or on a more consistent assessment of the rivals' threat requires further study. Thus, future investigations might focus in more detail on the accuracy of ranging in relation to the kind of degradation as well as to similarities of acoustic features among song types.

These arguments also might contribute to explaining differences between the present results and those with great tits (McGregor and Krebs 1984; also see Wiley and Godard 1996). In great tits only some song types have prominent tonal frequency sweeps and, in addition, song types cover a smaller frequency range compared to songs of Carolina wrens and Kentucky warblers. These features presumably impair assessment of frequency-dependent attenuation. In the experiment with great tits degraded songs used for playback were produced by broadcasting songs through the subjects' open and semi-open habitats so that they were presumably degraded primarily by frequency-dependent attenuation and irregular amplitude fluctuations (Richards and Wiley 1980). Thus, lack of features that are likely to enhance

assessment of degradation combined with variation in structure among song types might have contributed to an influence of familiarity with the song type on great tits' responses to playbacks of undegraded and degraded songs.

In conclusion, it is important to note that degradation of acoustic signals can vary considerably at the same distance dependent on microclimatic conditions, absolute and relative positions of sender and receiver (Dabelsteen et al. 1993; Mathevon et al. 1996; Mathevon 1997), and the exact nature of the propagation path. Wiley and Godard (1996), for instance, suggested that the uncertainties in degradation might limit accuracy of ranging much as does lack of familiarity with song features. Although we still have very limited information on the accuracy of ranging, it seems that lack of familiarity with a particular song type does not preclude approximate ranging of songs, either by reverberation or by the relative intensities of high frequencies. Importantly, ranging of approximate distance on the basis of one song seems to be sufficient to allow a bird to assess quickly if a rival is inside the territory, close to the boundary or outside the territory. Such general information on location is crucial at the outset, because the nature of subsequent response is affected primarily by whether or not the rival has intruded the territory. Finally, responses did not differ between familiar (neighbors') and unfamiliar (strangers') song for either playback treatment. This suggests that one song was not sufficient to allow a bird to assess reliably the identity of the simulated rival. This supports earlier suggestions that birds might initially attend to information on species and distance of a singer and might need to listen repeatedly to integrate additional information (Naguib 1996a).

Implications for communication

Ranging and song repertoires

Cues for ranging such as reverberation, changes in amplitude (Naguib 1997) and, under the constraints discussed above, the relative intensities of high-frequencies could be extracted, possibly with different accuracy, from parameters found in most birds' songs as discussed above. Thus, in line with arguments of McGregor (1994) and Wiley and Godard (1996), these results provide no evidence that individuals could increase fitness by singing songs that are "unrangeable" to receivers, as suggested by Morton (1982, 1986, 1996). In Morton's argument selection favors individuals that can sing songs that are unfamiliar to receivers and consequently cannot be ranged. Senders then would benefit by adding new, unrangeable songs to their repertoires. The proposed receiver's constraints on ranging would thus favor the evolution of song repertoires (Morton 1982, 1986). However, as none of the experiments conducted so far has yielded evidence to support the conclusions that

songs cannot be ranged unless in the listeners vocal repertoire (discussed in detail in McGregor 1994), it remains questionable if constraints on ranging have had a notable influence on the evolution of song repertoires.

Ranging and matched counter singing

Based on arguments that ranging requires prior familiarity with the song type, it has been suggested that birds involved in matched counter-singing (both individuals singing the same song pattern alternately during an interaction) might do so in order to exchange precise distance information (Krebs et al. 1981; Falls et al. 1982; McGregor and Falls 1984; McGregor 1991, 1994). By singing the same song pattern birds would provide each other with accurate information about their locations. As matched counter-singing mostly occurs during close-range interactions or boundary disputes, it in fact might be advantageous to provide the intended receiver with accurate information about location. The finding that Carolina wrens ranged song types which they were unlikely to have heard previously, however, does not seem to support this notion, unless familiarity with the song type enhances accuracy of ranging on a level we have not assessed yet. Although birds presumably can use general song features in order to assess degradation, as discussed above, they might be more accurate in assessing degradation of finer details when they can compare the degraded song to an undegraded auditory input with the same characteristics. Thus birds involved in matched counter-singing might not only do so in order to provide information to receivers but also to provide themselves with an auditory standard for more accurately assessing degradation (and possibly other features) in conspecific signals.

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