

RANGING OF CONSPECIFIC SONGS BY KENTUCKY WARBLERS AND ITS IMPLICATIONS FOR INTERACTIONS OF TERRITORIAL MALES

by

R. HAVEN WILEY¹⁾ and RENÉE GODARD^{2,3)}

(Department of Biology, University of North Carolina, Chapel Hill, NC 27599-3280, USA)

(Acc. 27-VI-1995)

Summary

Kentucky warblers (*Oporornis formosus*) each sing a single song pattern. To determine whether males could range (estimate the distance to) conspecific songs, we presented clean and reverberated versions of strangers' songs to 12 males in a factorial design. To assess differences between the playbacks and the subjects' own songs or neighbors' songs, we measured differences in minimal repetition periods between repeated acoustic elements in songs, features that could contribute to assessment of reverberation. Results indicated that Kentucky warblers can range conspecific songs and that similarity between playback songs and established neighbors' songs or a subject's own songs did not enhance this ability. Direct evidence that males misjudged the distance to reverberated playbacks excluded other interpretations of the results based on differences in the detectability or habituation of clean and reverberated songs. These results suggest further that assessment of reverberation is sufficient for ranging and that perceptual analysis of song is not necessarily linked to overt production. As a consequence, repertoires of songs do not necessarily promote interference between territorial neighbors.

Introduction

Following the original demonstration by Richards (1981), several studies have confirmed that passerines can range (judge the distance of) conspecific songs (McGregor *et al.*, 1983; McGregor & Falls, 1984; McGregor &

Krebs, 1984; Shy & Morton, 1986; Brindley, 1991; Naguib, 1995a, b). Each of these studies showed that clean versions of conspecific songs evoked stronger reactions than degraded versions presented at the same intensity and from essentially the same location. This difference in response to clean and degraded songs matches that expected for conspecific rivals respectively inside and outside the subjects' territories. Thus subjects evidently judged degraded versions of songs to come from farther away than clean ones.

Among species that have so far served as subjects for ranging experiments (Carolina wren *Thryothorus ludovicianus*, great tit *Parus major*, western meadowlark *Sturnella neglecta*, European robin *Erithacus rubecula*), individuals have repertoires of multiple songs and share song patterns with neighbors. Shared song patterns have particular relevance for ranging. In order to judge the distance to the source of a signal on the basis of its degradation during propagation, a listener must have information about the signal at the source for comparison with the received signal. Morton (1982, 1986) proposed that, to allow such a comparison, a bird must incorporate a song pattern into its own repertoire, so that it shares the pattern with the singer, before it can range it.

Most previous studies have provided evidence that a subject's familiarity with a song pattern enhanced its discrimination of clean and degraded versions. Nevertheless, McGregor & Krebs (1984) could find no indication that great tits ranged song patterns that they themselves produced any better than patterns sung by their neighbors. Evidently, perceptual familiarity with a song pattern, even without production of the pattern, allowed reliable ranging. None of these studies isolated any particular features of songs sufficient for ranging.

Unlike subjects of previous experiments on ranging, each Kentucky warbler (*Oporornis formosus*) has a single, distinctive song. Consequently, any ability to range songs cannot depend on incorporation of other individuals' song patterns in subjects' repertoires.

Songs of this species have additional relevance for studies of ranging. Unlike most forest species, which lack rapidly repeated elements at the same frequency (Wiley, 1991), Kentucky warblers' songs consist of repeated syllables which in turn consist of rapidly repeated elements (Tsipoura & Morton, 1988). This exception to the general rule for songs

¹⁾ Corresponding author.

²⁾ Present address: Biology Department, Hollins College, Roanoke, VA 24020, USA.

³⁾ We thank M. Green, P. McGregor, E.S. Morton, M. Naguib, and P.K. Stoddard for many insightful discussions of ranging by birds and helpful critiques of the manuscript.

of forest birds might represent an adaptation for ranging. Rapidly repeated elements at the same frequency could facilitate discrimination of levels of reverberation by providing standards for judging the intensity of reverberation at fixed intervals. Because reverberation is a major source of acoustic degradation in forests, rapidly repeated elements at the same frequency might promote accurate ranging of songs in forests.

Kentucky warblers' songs differ somewhat among individuals in the repetition intervals of elements within syllables. Consequently, subjects might range a song more accurately if it had familiar repetition intervals. For instance, songs with intervals similar to those of neighbors' or its own songs might permit more accurate ranging.

The structure of Kentucky warblers' songs thus suggests adaptations to promote accurate ranging. In contrast, each male's unique song pattern suggests, by Morton's reasoning, impediments to accurate ranging. To investigate the possibility of ranging in this species, we presented playbacks of tape recordings to create the impression of a strange male appearing in a previously unoccupied location, either at the edge of the subject's territory or well beyond the edge.

Because reverberation is such a prominent source of degradation of acoustic signals in forests (Richards & Wiley, 1980; Wiley & Richards, 1982; Wiley, 1991), we explored the possibility that Kentucky warblers can range songs on the basis of reverberation alone. We also evaluated any effects of the subjects' familiarity with the repetition intervals between syllables and between elements within syllables on their responses to the songs presented. A factorial experimental design allowed us to evaluate of the influences of different song exemplars, order of presentation, and degree of degradation on the subjects' responses.

Methods

General methods

Our experiments presented clean and reverberated versions of the same songs to territorial males. We prepared 6 playback tapes: clean and reverberated versions of three exemplars of songs (Fig. 1). Each of the three pairs of clean and reverberated tapes was then presented to four subjects. Two received the clean version first, and two received the reverberated version first. Thus a total of 12 subjects each received two playbacks for a total of 24 playbacks. This design, which replicated each combination of treatment (clean and reverberated), order of presentation (first or second), and exemplar, allowed us to analyze statistically the influ-

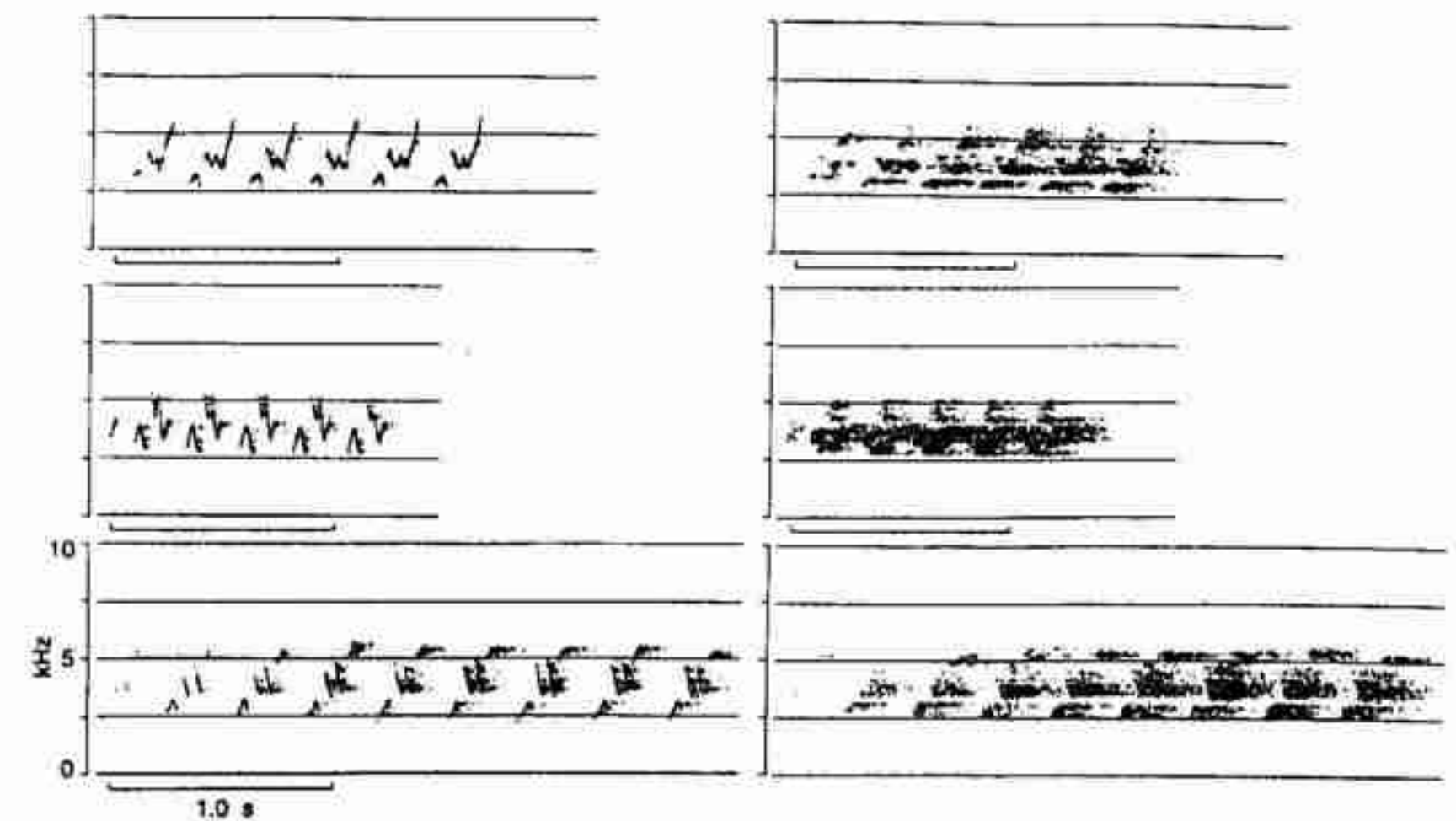


Fig. 1. Spectrograms of clean (left) and reverberated (right) versions of three male Kentucky warblers' songs used for playback. Note the repetition of syllables, each of which includes repetition of nearly identical elements. Clean songs recorded at 8-12 m include minimal reverberation; reverberated songs include levels of reverberation similar to recordings at 100 m or more. Horizontal lines at 2.5 kHz intervals; major time marks at 0.5 s. All spectrograms prepared with identical parameters to allow comparison of reverberations.

ences of these factors and their first-order interactions on subjects' responses. A factorial design of this sort is the best method for evaluating variance in responses to the different songs used as exemplars in an experiment (McGregor *et al.*, 1992). In addition, we could examine in a limited way the possibility of individual differences among subjects.

Our subjects consisted of male Kentucky warblers on territories in the Mason Farm Biological Reserve near Chapel Hill, North Carolina, and adjoining areas. Here this species inhabits mature bottomland hardwood forests with thick layers of shrubs and ground cover. Beginning on 23 April 1991, shortly after most males had arrived, we mapped singing males' locations and taperecorded their songs with a Sony TC-D5M cassette recorder and a Sennheiser K3U/ME88 directional microphone. Studies of individually marked males in previous years confirmed that each male in this population sang a single individually distinctive pattern, similar to those reported for other populations (Morton & Young, 1986; Tsipoura & Morton, 1988). Two males in 1991 retained color bands from previous years, but males were separated primarily by their locations and distinctive songs.

Procedures for playbacks

Between 14 and 21 May 1991 each subject received two playbacks 60-85 min apart, one clean and one reverberated recording of the same song. No male heard recordings of its own or a neighbor's songs. We chose the playback tapes for each subject by the roll of

a die after positioning the speaker, subject to the constraint that each of the three pairs of clean and reverberated tapes was presented to four subjects, twice with the clean version first and twice with the reverberated version first.

For each playback, we placed the speaker 50-100 m from the subject, at a location just outside the limits (within 25 m) of the area used by the subject for singing and in some direction other than toward an established territorial neighbor. Most males sang in areas 150-250 m in diameter and had 1-2 contiguous territorial neighbors, so meeting these constraints on location was not difficult. The speaker was clamped to a small tree 1.8-2.0 m above ground and aimed toward the subject.

As a precondition for beginning a playback, the subject had to continue singing at the prescribed distance of 50-100 m for at least one minute while no neighbors sang within hearing. Four additional subjects received similar playbacks after one minute of repeated calls (vocalizations other than song) by either the subject or his mate. These males showed no indication of responding to either of the two playbacks (no approach, no change in calling). We therefore restricted these experiments to subjects that were actually singing when each playback began. During dates of the experiments most males had nests with young, a period when they usually sang or called in bouts lasting several minutes once every 30-60 min during the morning. Thus we normally met the precondition within an hour of our arrival in a male's territory. No experiment began before 06:50 (EDT), to avoid the period of singing near dawn, and none continued past 12:10.

Because we were interested in the possibility that males might judge the distance to a singer by ear, we prevented a subject from obtaining any close-range experience with the speaker. So the moment a male appeared within 15 m of the speaker, we stopped the playback. This rule meant that 16 of the 24 playbacks terminated after fewer than 10 songs; one included only one song before the subject approached. In all previous studies of ranging, playbacks continued for a predetermined time (Richards, 1981; McGregor *et al.*, 1983; McGregor & Falls, 1984; McGregor & Krebs, 1984; Shy & Morton, 1986; Brindley, 1991). As a consequence, subjects often approached the speaker well before its termination. This situation makes it difficult to interpret responses solely in terms of capabilities for ranging songs at a distance. To reduce this problem, we prevented subjects from approaching the playback closely (see also Naguib, 1995a, b). Our procedure thus standardized close-range experience with the stimulus, rather than total duration of the stimulus.

Playback tapes

Three males' songs, recorded from distances of 8-12 m at locations 500 m or more apart near the Mason Farm Biological Reserve, were used for preparation of playback tapes (Fig. 1). These three songs were selected from clean recordings to exemplify the range of variation in structure of songs in this population. Each exemplar was digitized with 12-bit accuracy and then reconverted to an analog signal and recorded on a Marantz PMD221 recorder. These three clean playback tapes had the same recording levels on the VU-meter of the recorder.

Males normally sang at rates of 3-6 songs/min. Because we did not wish to evoke strong responses from the subjects, we selected a rate of 3 songs/min for the playbacks. The intervals between songs matched an actual sequence by an undisturbed singing male

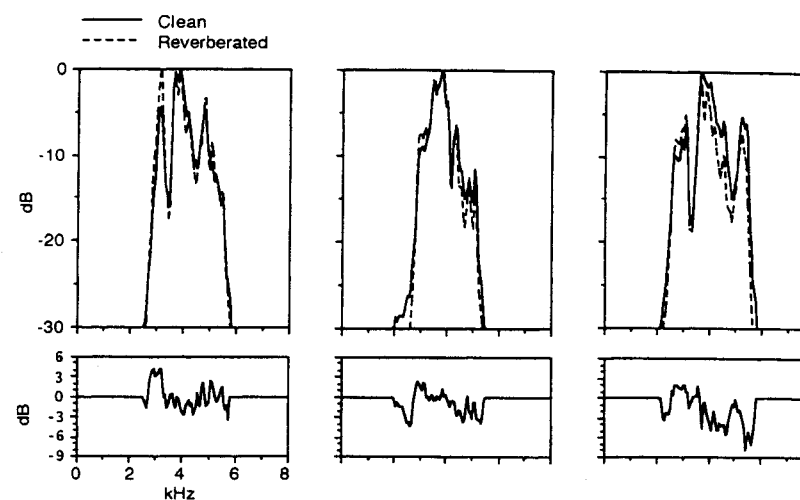


Fig. 2. Power spectra of clean (solid line) and reverberated (dashed line) versions of songs used for playback (above) and their difference spectra (reverberated version minus clean version) (below).

and thus varied somewhat. The same intervals were used for each playback tape to produce a sequence of 10 songs lasting 3 min.

Each of the three clean playback tapes was then used to prepare a reverberated tape (Fig. 1) by playing it back and re-recording it in a large attic. This room, approximately 35 × 15 m with no large parallel surfaces to create standing waves, served as a complex reverberation chamber. By adjusting playback and re-recording positions between distances of 6-10 m over cluttered objects, while monitoring the re-recorded signal with an oscilloscope, we could obtain repeatable levels of reverberation with decay rates similar to those after propagation through 100 m of forest. The short propagation distances and the absence of wind made irregular amplitude fluctuations negligible. The overall spectra of the three songs before and after broadcast differed by ±4-5 dB (Fig. 2), but there was no consistent pattern of high-frequency attenuation (Figs 1, 2). The complex reverberation closely matched that in a forest.

For re-recording the reverberated tapes we used the same Marantz PMD221 recorder mentioned above and a Sennheiser K3U/ME80 cardioid microphone. Recording levels were adjusted to maintain the same VU-meter readings as on the clean tapes.

In the field, we used the line output of a Sony TC-D5M recorder connected through a Perma-Power S702 portable amplifier and an 8-m cable to the speaker (Realistic tweeter horn, frequency response ±3 dB, 2-10 kHz). Before the experiments, we determined the amplifier gain necessary to obtain 90 dB at 1.0 m from the speaker for each tape in a virtually anechoic environment (above herbaceous vegetation 1.5-m deep in the center of a

large field on a still day, with a Realistic 332050 SPL meter, fast response, C-weighting). These gains were then used for the playbacks.

Behavioral measures

During previous experiments (Godard, 1991), male Kentucky warblers responding to playbacks within or near their boundaries usually abruptly ceased singing, flew to the speaker, flew back and forth over or near the speaker while playbacks continued and for several minutes afterward, and eventually started a prolonged bout of singing after playback stopped. Males often uttered distinctive *tsuk* calls during and after playbacks, although they usually remained silent when most agitated. Similar behavior occurred when two males interacted at close range. In contrast, the response to singing well outside a male's territory consisted of countersinging often accompanied by gradual approach to the boundary during prolonged interactions.

During our experiments we dictated into a hand-held cassette recorder all changes in the subject's distance and direction from the speaker, all songs by the subject, and all flights >1 m within 15 m of the speaker (the greatest distance at which we could reliably see the birds). From these dictations, we determined the following measures of a subject's behavior: (1) the latency to approach within 15 m; (2) the time within 15 m of the speaker during a 10-min period following the playback; (3) the closest approach to the speaker in a horizontal direction; (4) the number of flights within 15 m of the speaker for 10 min following the playback; (5) the number of songs during the playback (because males usually stop singing once they approach the speaker, this measure correlates with the latency for approach); (6) the number of songs for 10 min following playback; (7) the time spent beyond the speaker (with reference to the subject's original position) during the 10-min period following the playback; and (8) whether or not the male flew past the speaker from >15 m away in its original direction to >10 m away in the opposite direction within 30 s of the onset of playback (termed 'flying past'). We chose these last two measures as direct indications that the subject had misjudged the distance to the playbacks.

Differences between the playback song and the subject's or its neighbors' songs

Because our interest lay in the possible use of reverberation to judge the distance to a singer, we focused on the feature of songs that was most likely to be affected by reverberation. Reverberation reduces a listener's ability to discriminate closely spaced elements at approximately the same frequency. Kentucky warblers' songs consist of similar, repeated syllables, each of which includes similar, repeated elements (Tsipoura & Morton, 1988; Fig. 1). To compare these features of the songs of each subject with those of each of the three exemplars for playback tapes, we computed differences in (1) the repetition periods (intervals between onsets) of similar elements within syllables and (2) the repetition periods of syllables. These measurements were taken from spectrograms displayed on a Uniscan II real-time spectrum analyzer with 6.25-ms resolution.

Each subject had one or two contiguous neighbors. For measures of the difference between each subject's neighbors' songs and the playback, we chose that neighbors' songs that most closely resembled the playback. Presumably the most similar neighbors' songs provided experience relevant to ranging the playback.

Statistical analysis

To compare each of our measures of response to clean and reverberated playbacks, we used Wilcoxon matched-pairs signed-ranks tests. Although these separate analyses allow clear interpretations, they do not provide the best overall statistical assessment of the results because the different behavioral measures of response were correlated with each other to varying degrees. In addition, the experimental conditions, including exemplars of songs used for playback, were replicated. Consequently, we used SYSTAT (Wilkinson, 1988) to extract principal components from the first seven measures listed above. The scores on the first principal component then served as overall measures of response, the dependent variable in further statistical analyses. For these analyses, we used the multivariate general linear hypothesis implemented by SYSTAT (Wilkinson, 1988), equivalent to analyses of variance, when all independent variables were categorical, or analyses of covariance, with continuous independent variables as covariates. Replication of treatments allowed us to assess differences between subjects, orders of presentation, and exemplars of songs used for playback, as well as the difference between clean and reverberated songs.

Results

Separate analyses of behavioral measures

Clean playbacks elicited fewer songs during and after playback, shorter latencies for approach, more flights near the speaker, closer approach, less time spent beyond the speaker, and more time spent near the speaker after the playback than did reverberated playbacks (Fig. 3). In Wilcoxon matched-pairs signed-ranks tests, only two of these measures (number of flights and time near the speaker after playback) differed significantly between clean and reverberated playbacks (Fig. 3). However, the means of all eight behavioral measures of responses differed between clean and reverberated playbacks in accordance with expectations for responses to intruding and distant rivals, respectively. In response to clean playbacks, subjects tended to cease singing and approached their presumed rival.

Our two direct measures of misjudgments of distance also fit expectations for clean and reverberated playbacks. Time spent beyond the speaker was greater following reverberated playbacks, although not significantly so. Also, on their first appearance, subjects flew past the speaker more often in response to reverberated than to clean playbacks (4 and 0 occasions, respectively). Thus, even though they were less likely to approach a reverberated playback, when they did, they often flew past it. In three cases the subject disappeared far beyond the speaker. By ranking responses for

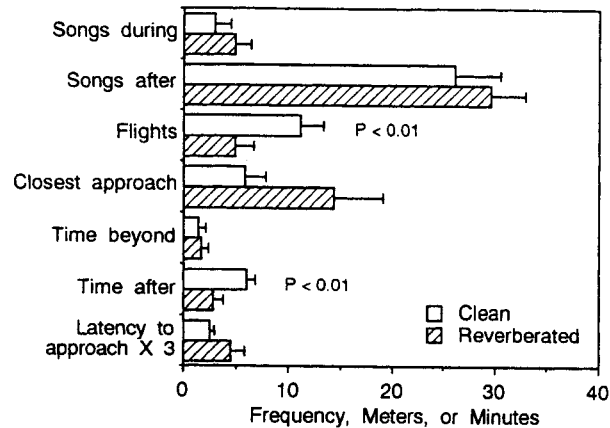


Fig. 3. Means and SE's for each of seven behavioral measures of response to clean and degraded playbacks. See text for definitions of the behavioral measures. Probabilities indicate significance in Wilcoxon matched-pairs signed-ranks tests.

a Wilcoxon signed-ranks paired comparison, to take advantage of our experimental design with paired presentations of clean and reverberated tapes from the same locations, the difference was nearly statistically significant ($p < 0.062$, one-tailed, because antecedent considerations led us to predict flying past reverberated songs). Thus our subjects did in fact behave as if they judged the reverberated playbacks to be farther away than they actually were.

Extraction of principal components

Correlations among the first seven behavioral measures of responses to the playbacks ranged from 0.77 to -0.62 . The first principal component extracted from the correlation matrix explained 49.7% of the variance in responses. The second component explained only an additional 16.8% of the variance. Consequently, we used the scores for the first principal component as our primary measure of the subjects' responses. The loadings of the seven behavioral measures on the first principal component were as follows: latency to approach (0.87); closest approach (0.84); number of songs during playback (0.82); number of songs after playback (0.37); time spent beyond the speaker (-0.31); number of flights (-0.72); and

time spent within 15 m after the playback (-0.76). The number of songs during playback correlated closely with latency to approach, because subjects normally ceased singing when they approached the speaker. Negative scores on the first principal component indicated responses with short latency, close approach, few songs during playback, many flights, and long periods near the speaker following playback, the usual pattern of responses to an intruder inside the territory.

Analysis of variance in responses

The first principal component of our behavioral measures was the dependent variable in analyses of variance. Because our factorial design replicated each combination of treatment (clean or reverberated), order of presentation, and exemplar of songs, we could examine variance in responses associated with each of these factors and their interactions. In this analysis, only treatment had a significant effect on responses (Table 1). The mean scores on the first principal component of our behavioral measures were lower (stronger response) for clean recordings than for reverberated ones.

The three exemplars included songs with 5, 6, and 8 syllables (Fig. 1); they also differed slightly in the amount of residual reverberation in the close-range recording used for the 'clean' treatment (Fig. 1). Nevertheless, there were no consistent differences in responses to these three exemplars of songs. The 5-syllable exemplar received the weakest response on aver-

TABLE 1. Analysis of variance in responses to playbacks: effects of exemplars of songs for playback, order of presentation, treatments (clean or reverberated) and their interactions on the first principal component of measured responses

Variable	Mean square	df	F	p
Treatment	3.69	1	5.39	0.04
Exemplar	2.23	2	3.26	0.07
Order	2.13	1	3.11	0.10
Treatment × Exemplar	0.71	2	1.04	0.38
Treatment × Order	0.87	1	1.27	0.28
Exemplar × Order	0.42	2	0.62	0.55

age among both clean and reverberated playbacks; the 6-syllable exemplar evoked the strongest responses on average among clean playbacks, but the 8-syllable evoked the strongest response among reverberated playbacks. The analysis of variance showed neither a significant main effect of the exemplar used for playback, nor a significant interaction between exemplar and treatment. Order of presentation also had no effects on responses (Table 1).

Familiarity with repetition periods in songs

It was not possible to include in one analysis of covariance all four measures of differences in minimal repetition periods between the playback and the subjects' or neighbors' songs. We thus conducted four exploratory analyses of covariance, each of which included only one of our four measures. Variables that had no probable main effects or interactions ($p > 0.1$) in these preliminary analyses were then eliminated from a final analysis.

Each exploratory analysis included the following independent variables: treatment (two categories, clean and reverberated), exemplars of songs for playback (three categories, the songs used to prepare playback tapes), order of presentation (two categories, first and second), and one of the four measures of the difference in minimal repetition periods (between the playback and either the subject's or its neighbors' songs, for either syllables or elements within syllables, each measure a continuous covariate). In addition, each analysis included all six first-order interactions. The dependent variable in these analyses was the first principal component of our measures of response.

Four variables survived elimination in these exploratory analyses: treatments; exemplars of songs for playback; the difference between the playback and the subject's own songs in the minimal repetition interval of elements within syllables; and the analogous measure of the difference between the playback and the most similar neighbor's songs. An analysis of variance with these four variables allowed us to compare the effects of differences between playbacks and either subjects' or neighbors' songs.

In these analyses, none of the four main effects approached significance, but three interactions did (Table 2): (1) responses to the two treatments varied with the exemplar used for playback; (2) responses to the three exemplars varied with their differences from the subject's songs; and (3) re-

TABLE 2. Analysis of covariance for the first principal component of responses: effects of treatment (clean or reverberated playback tapes), exemplar of songs for playback, and differences in minimal repetition periods (of elements within syllables) between the playback and either the subject's song or the most similar neighbor's song

Variable	Mean square	df	F	p
Treatment	0.58	1	1.98	0.19
Exemplar	0.51	2	1.73	0.23
Difference from subject's song	0.46	1	1.55	0.24
Difference from neighbors' songs	0.69	1	2.35	0.16
Treatment \times Exemplar	1.85	2	6.31	0.017
Treatment \times Subject's difference	0.56	1	1.90	0.20
Treatment \times Neighbors' difference	3.83	1	13.01	0.005
Exemplar \times Subject's difference	1.79	2	6.10	0.019
Exemplar \times Neighbors' difference	0.58	2	1.97	0.19

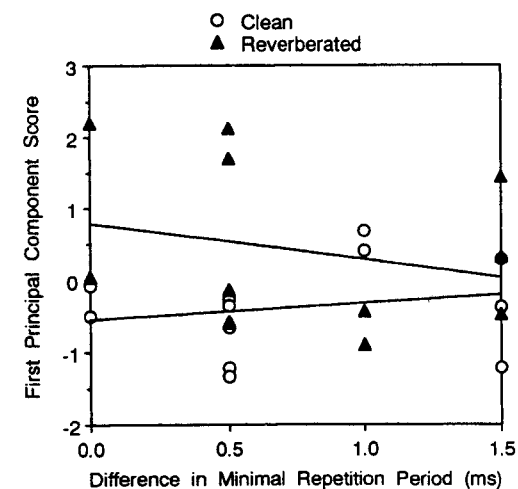


Fig. 4. Responses (first principal component scores) to clean and reverberated playbacks as a function of the difference between the playbacks and the most similar neighbors' songs. Stronger responses have more negative scores on the first principal component. The lines represent regressions through the two sets of points. The interaction between differences between songs and treatment (clean or reverberated) is statistically significant (see text). Playbacks that differed from neighbors' songs evoked strong responses if clean but weak responses if reverberated.

sponses to the two treatments depended strongly on the difference between the playback and the most similar neighbor's song. Because our exploratory analyses considered a total of four differences between the playback and the subjects' or neighbors' songs, a conservative approach would divide the acceptance level by 4, so $\alpha = 0.05/4 = 0.0125$. The first two interactions above do not meet this criterion (Table 2). The third interaction is thus the clearest result: the subjects discriminated more between clean and reverberated playbacks when the playbacks differed more in the minimal repetition interval of elements within syllables from the most similar neighbor's songs.

The absence of a main effect of treatment arose because clean and reverberated songs evoked opposite patterns of response (Fig. 4): reverberated playbacks evoked weaker responses, but clean songs evoked stronger responses, when more divergent from neighbors' songs. Note the opposite trend (although not statistically significant) for the interaction between treatment and difference between the playback from the subject's own songs (Fig. 5).

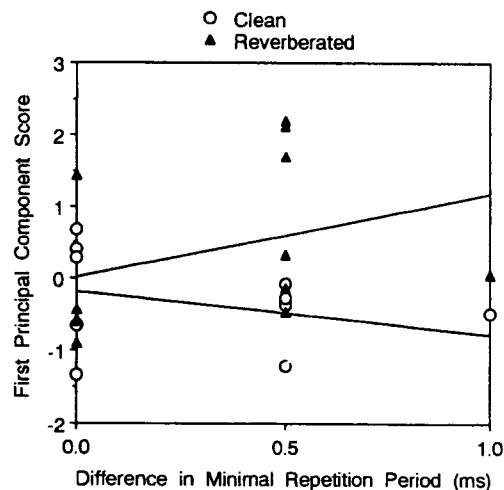


Fig. 5. Responses (first principal component scores) to clean and reverberated playbacks as a function of the difference between the playbacks and the subjects' own songs. Stronger responses have more negative scores on the first principal component. The lines represent regressions through the two sets of points. The interaction between differences between songs and treatment (clean or reverberated) is not statistically significant (see text).

Analyses of variance or covariance are particularly sensitive to outliers in the data. A plot of expected values vs residuals (Wilkinson, 1988) for the preceding analysis revealed no clearly separated outliers. Two residuals with values just over 2 SD's from the mean (symmetrically above and below the mean) were marginally improbable in a sample of 24. When these two points were deleted from the analysis, the influence of the exemplars of songs for playback became clearer, but the influences of the differences between the playbacks and the subjects' or the neighbors' songs remained virtually the same. The interaction between treatment and difference from neighbors' songs remained significant ($p = 0.005$); the interaction between treatment and difference from the subjects' own songs remained non-significant ($p = 0.192$). The conclusion thus appears to be robust: subjects discriminated most clearly between clean and reverberated playbacks when playbacks differed from neighbors' songs.

Discussion

Can Kentucky warblers range conspecific songs?

Our results show that Kentucky warblers respond differently to degraded and undegraded conspecific songs. After the initial demonstration by Richards (1981) that Carolina wrens can discriminate between degraded and undegraded songs, similar discriminations were reported in great tits, western meadowlarks and European robins (McGregor *et al.*, 1983; McGregor & Falls, 1984; McGregor & Krebs, 1984; Shy & Morton, 1986; Brindley, 1991). In all cases, territorial males responded less vigorously to degraded than to undegraded songs, as do Kentucky warblers.

As first noted by Richards (1981), there are two possible interpretations of diminished responses to degraded, in comparison to clean, playbacks. The subject might have a lower probability of detecting or recognizing the signal and thus have a lower probability or longer latency of response. In this case, degradation reduces detection or recognition of the signal. Alternatively, the subject might detect degraded and clean signals nearly equally but respond to degraded ones less intensely because they judged them to come from farther away. Degradation, in this case, serves as a cue for ranging.

Subsequent studies have also considered this issue. Experiments with great tits, western meadowlarks, and European robins have all compared responses to degraded and clean songs both familiar and unfamiliar to the subjects (McGregor *et al.*, 1983; McGregor & Falls, 1984; McGregor & Krebs, 1984; Brindley, 1991). In these cases, subjects responded nearly alike to degraded and clean unfamiliar songs but significantly differently to degraded and clean familiar ones. The first result suggests that detectability had no significant influence on responses, while the second suggests that familiarity with a stimulus enhanced ranging (McGregor & Krebs, 1984).

The results for great tits are especially persuasive, because the familiar and unfamiliar songs were all songs of strangers (McGregor & Krebs, 1984; McGregor, 1994). The familiar songs represented relatively minor variants of patterns sung by the subjects' neighbors; the unfamiliar songs belonged to patterns not used by neighbors. Thus subjects heard only the songs of strangers, some of which resembled those of neighbors. Because any stranger's songs presumably represented the same threat to a territorial male, differences in responses would result entirely from effects of familiarity on ranging.

This interpretation of the results for great tits nevertheless remains problematic. It seems plausible that subjects might often confuse strangers' songs similar to neighbors' with neighbors' songs, at least temporarily, so that responses to these playbacks would resemble normal interactions with neighbors. Responses to apparent neighbors might depend on location. On the other hand, subjects might respond to easily recognized strangers without regard to location. In this interpretation, familiarity would influence a subject's attitude toward a singer's location but would not influence its ability to judge a singer's distance.

Another possibility is that subjects' responses to these playbacks reflect a generalization gradient of habituation. Subjects most frequently experience neighbors' songs degraded by distance. A clean version of a neighbor's song or any unfamiliar song might elicit greater responses because they occur less frequently. The results obtained with European robins fit the pattern expected from habituation: approximately equally strong responses to all songs except degraded neighbors' songs (Brindley, 1991). Differences in familiarity of songs could produce other patterns of response as well,

depending on the generalization gradients for recognition and habituation of clean and degraded songs.

In an effort to clarify interpretation of these results, our experiments incorporated two innovations. First, by terminating each playback as soon as the subject approached the speaker, we reduced the possibility that subjects' responses were influenced by close-range exposure to the playback. An even clearer procedure would present a single song at a standardized distance from a subject (Naguib, 1995a). In any case, evidence for ranging should only include responses to presentations at a standardized distance.

In a second innovation to clarify conclusions about ranging, we tried two possibilities for direct indications that subjects had misjudged the distance to the speaker. The first of these measures, the time spent beyond the speaker after playback, did not differ significantly between reverberated and clean playbacks. After approaching the speaker, which occurred more often in response to clean playbacks, subjects apparently searched in the general vicinity for a rival. A clearer measure of misjudging the distance to the speaker might have used the time spent at least some minimal distance beyond the speaker.

The second of our direct measures, immediate flights to locations well past the speaker, focused on the subjects' first observable responses. Although our subjects tended not to approach reverberated playbacks quickly, when they did their behavior was dramatic. A direct flight past and at least 10 m beyond the speaker in the interval following the first reverberated playback unambiguously indicated that the subject had overestimated the range of degraded songs. Naguib (1995a) recently obtained similar responses to degraded songs of Carolina wrens. This direct evidence for ranging strengthens the interpretation, shared with previous studies, that different intensities of response to clean and degraded songs indirectly indicate abilities to range conspecifics' songs.

Does familiarity with songs influence ranging?

Most studies of ranging have found clearer discrimination between clean and degraded songs when songs were familiar than when they were unfamiliar. However, the conclusion that familiarity enhances ranging is again problematic, for reasons similar to those just noted. In particular, subjects might habituate to familiar patterns, they might detect or recognize familiar

patterns more reliably than unfamiliar ones, or location might have more influence on responses to familiar than unfamiliar songs. Furthermore, subjects might partially confuse songs resembling neighbors' with actual neighbors' songs. Habituation in combination with difficulties of detection could explain any ranking of responses to clean and degraded familiar and unfamiliar songs.

In the experiments with great tits, resemblance to neighbors' or the subjects' own songs was assessed subjectively by a panel of judges (McGregor & Krebs, 1984), without regard to features of the song that might be affected by degradation, such as minimal rates of repetition or range of frequencies. A stronger prediction for the relevance of familiarity to ranging would come from comparisons of these specific features of songs.

The Kentucky warbler provides a candidate for this sort of comparison. The rapidly repeated elements in their songs are unusual in the songs of forest birds (Richards & Wiley, 1980; Wiley, 1991). Their presence might enhance ranging by facilitating judgments of the degree of reverberation (Wiley & Richards, 1978, 1982; Wiley, 1991). If so, the relevant parameters to judge the similarity of songs are the minimal repetition periods between similar acoustic elements. A disadvantage of this approach is the limited variation available for study. The variation is inevitably less for differences between the playback and any neighbors' songs than for differences between the playback and the subjects' songs, because subjects often have two or three neighbors, any of which might resemble the playback.

Our examination of the differences between the playbacks and the subjects' neighbors' songs provided no evidence that familiarity enhanced ranging. Instead, our results indicate that subjects discriminated most clearly between clean and reverberated songs when the playbacks *differed* from their neighbors' songs. The stimulus evoking the strongest responses by our subjects was a clean song with unfamiliar intervals within syllables; the stimulus evoking the weakest responses was a reverberated song with unfamiliar intervals. Songs with familiar intervals, whether clean or reverberated, evoked intermediate responses. Furthermore, differences between the playbacks and the subjects' own songs had no consistent influence on responses.

The greater difference between responses to degraded and clean songs with unfamiliar features than to such songs with familiar features is just

the opposite of the result obtained with great tits. Possibly Kentucky warblers, with their large territories, are more concerned about the locations of strangers than of neighbors, whereas great tits on much smaller territories are just the opposite. Our results, like those with the great tits, might also be explained by a combination of recognition and habituation. A degraded unfamiliar song might have been less likely to catch the subject's attention, while a clean unfamiliar song might have evoked a maximal response because of minimal habituation. Either interpretation would also explain intermediate levels of response to degraded or clean songs with familiar features.

Our examination of the differences between the playbacks and the subjects' own songs revealed a trend, although not a significant one, for greater differences in responses to clean and degraded songs that resembled the subjects' songs. This trend is the one predicted by Morton's (1986) hypothesis that a bird must have a song in its own repertoire in order to judge its distance. Nevertheless, our experiments failed to demonstrate that this familiarity with the features of a song significantly improves discrimination of clean and degraded playbacks by Kentucky warblers. It remains possible that familiarity with the structure of particular songs affects the accuracy of this discrimination, and hence of ranging, at a level that we cannot yet assess. Our results with Kentucky warblers only indicate that lack of familiarity with the exact acoustic structure of the playbacks did not grossly interfere with ranging.

Precise information about the structure of a signal at the source would improve perception of reverberation and frequency-dependent attenuation, as well as any other features of the signal. Nevertheless, it seems unlikely that judging the approximate distance to a conspecific singer would require experience with particular song patterns. Experience with any conspecific songs could provide information about their general features, such as species-typical frequency spectra or absence of reverberation-like decays, and thus allow an assessment of frequency-dependent attenuation or reverberation. Alternatively, information about species-typical features of songs could be innate. Naive Carolina wrens, for instance, can discriminate between clean and degraded songs (Morton *et al.*, 1986).

Precision in estimating degradation of signals would also require information about the properties of the particular path of transmission. Some

general expectations about transmission might require only basic information about the structure of the habitat, but detailed information about transmission in a particular area might require actual experience there. Within any one habitat there is often substantial variation in transmission properties, but we lack information about its spatial or temporal scales. Thus accurate ranging of conspecific songs by a territorial bird might depend at least as much on familiarity with the acoustic properties of its territory as on familiarity with the songs of its neighbors.

What acoustic features are used for ranging?

Previous studies of ranging have used degraded songs prepared by broadcasting and re-recording songs in natural environments. Propagation of complex acoustic signals through forests adds both reverberation and frequency-dependent attenuation (Richards & Wiley, 1980; Wiley & Richards, 1982). Our tapes of degraded songs differed from those of clean songs in reverberation but not consistently in frequency-dependent attenuation. The three exemplars of songs evoked no significant differences in response, and differences in responses to clean and reverberated versions of each exemplar showed no relationship to the number of syllables, amount of residual reverberation in the clean version, or pattern of frequency-dependent attenuation. Consequently, our results suggest that Kentucky warblers can judge the distance to singing conspecifics on the basis of reverberation alone. Nevertheless, because we did not completely eliminate frequency-dependent attenuation from the degraded songs, this conclusion remains tentative.

Recent experiments have shown that Carolina wrens can use either form of degradation to judge the distance of conspecific songs in the field (Naguib, 1995b). Humans in laboratory settings can judge auditory distance by reverberation alone, although not by frequency-dependent attenuation alone (Mershon & King, 1975).

Production and perception of songs and the relationships of territorial neighbors

Because differences between the playbacks and the subjects' own songs had no consistent influence on discrimination between clean and reverberated songs, our results provide no evidence that intricate perceptual analysis of

a song requires production of the same or a similar pattern (Williams & Nottebohm, 1985; Margoliash & Konishi, 1985; Margoliash, 1986; Nottebohm *et al.*, 1990). Recognition of neighbors and discrimination of songs likewise involves detailed perception of songs without overt production of similar patterns (McGregor & Avery, 1986; Stoddard *et al.*, 1992; Godard, 1993).

As a consequence, there is no clear evidence that birds must enlarge their repertoires by matching their neighbors in order to range their songs (Morton, 1982, 1986). A report by Morton & Young (1986) that Kentucky warblers can alter the emphasized frequencies in their songs does not alter these conclusions. Even if corroborated, a rudimentary matching of the frequency ranges in songs of neighbors would not alter the prediction from Morton's (1982, 1986) ranging hypothesis that individually distinctive songs prevent ranging (Tsipoura & Morton, 1988, p. 15). Our results show that familiarity with song patterns, whether produced or not, does not improve ranging of songs by Kentucky warblers. Consequently, territorial males cannot interfere with their neighbors by producing songs that are less familiar to neighbors.

Conclusions

Direct indications that subjects misjudged the locations of playbacks provide the strongest evidence for ranging. Interpretation of different intensities of response to clean and degraded playbacks must consider the consequences of degradation for habituation, detection, and recognition of signals as well as ranging. These confounding alternatives also arise in interpreting the influence of familiarity with particular songs on responses to clean and degraded playbacks. Our results show that territorial Kentucky warblers can range conspecifics' songs, at least approximately, regardless of familiarity with the song pattern. Kentucky warblers differ from species in previous studies of ranging in having a single song pattern each and from most other birds inhabiting forests in incorporating rapidly repeated elements in their songs. The latter attribute might be an evolutionary adaptation to facilitate ranging.

References

- Brindley, E.L. (1991). Response of European robins to playback of song: neighbour recognition and overlapping. — *Anim. Behav.* 41, p. 503-512.
- Godard, R. (1991). Individual recognition by migratory songbirds. — PhD thesis, University of North Carolina, Chapel Hill.
- (1993). Tit for tat among neighboring hooded warblers. — *Behav. Ecol. Sociobiol.* 33, p. 45-50.
- Margoliash, D. (1986). Preference for autogenous song by auditory neurons in a song system nucleus of the white-crowned sparrow. — *J. Neurosci.* 6, p. 1643-1661.
- & Konishi, M. (1985). Auditory representation of autogenous song in the song system of white-crowned sparrows. — *Proc. Natl. Acad. Sci. USA* 82, p. 5997-6000.
- McGregor, P.K. (1992). Design of playback experiments: the Thornbridge Hall NATO ARW consensus. — In: *Playback and studies of animal communication* (P.K. McGregor, ed.), Plenum, New York, p. 1-9.
- (1994). Sound cues to distance: the perception of range. — In: *Perception and motor control in birds* (M. Davies & P.R. Green, eds). Springer, Berlin, p. 74-94.
- & Avery, M.I. (1986). The unsung songs of great tits (*Parus major*): learning neighbours' songs for discrimination. — *Behav. Ecol. Sociobiol.* 18, p. 311-316.
- & Falls, J.B. (1984). The response of western meadowlarks (*Sturnella neglecta*) to the playback of undegraded and degraded songs. — *Can. J. Zool.* 62, p. 2125-2128.
- & Krebs, J.R. (1984). Sound degradation as a distance cue in great tit (*Parus major*) song. — *Behav. Ecol. Sociobiol.* 16, p. 49-56.
- , — & 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, p. 898-906.
- Mershon, D.H. & King, L.E. (1975). Intensity and reverberation as factors in the auditory perception of egocentric distance. — *Percep. Psychophys.* 18, p. 409-415.
- Morton, E.S. (1982). Grading, discreteness, redundancy, and motivation-structural rules. — In: *Acoustic communication in birds*, Vol. 1 (D.E. Kroodsma & E.H. Miller, eds). Academic Press, New York, p. 183-212.
- (1986). Predictions from the ranging hypothesis for the evolution of long distance signals in birds. — *Behaviour* 99, p. 65-86.
- & Young, K. (1986). A previously undescribed method of song matching in a species with a single song 'type', the Kentucky warbler (*Oporornis formosus*). — *Ethology* 73, p. 334-342.
- , Gish, S.L. & Vander Voort, M. (1986). On the learning of degraded and undegraded songs in the Carolina wren. — *Anim. Behav.* 34, p. 815-820.
- Naguib, M. (1995a). Perception of auditory distance in song birds. — PhD thesis, University of North Carolina, Chapel Hill.
- (1995b). Auditory distance assessment in Carolina wrens (*Thryothorus ludovicianus*): the role of reverberation and frequency-dependent attenuation of conspecific song. — *Anim. Behav.*, in press.
- Nottebohm, F., Alvarez-Buylla, A., Cynx, J., Kim, J., Ling, C.-Y., Nottebohm, M., Suter, R., Tolles, A. & Williams, H. (1990). Song learning in birds: the relation between perception and production. — *Phil. Trans. Roy. Soc. London B* 329, p. 115-124.
- Richards, D.G. (1981). Estimation of distance of singing conspecifics by the Carolina wren. — *Auk* 98, p. 127-133.
- & Wiley, R.H. (1980). Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. — *Am. Nat.* 115, p. 381-399.
- Shy, E. & Morton, E.S. (1986). The role of distance, familiarity and time of day in Carolina wren responses to conspecific songs. — *Behav. Ecol. Sociobiol.* 19, p. 393-400.
- Stoddard, P.K., Beecher, M.D., Loesche, P. & Campbell, S.E. (1992). Memory does not constrain individual recognition in a bird with song repertoires. — *Behaviour* 122, p. 274-287.
- Tsipoura, N. & Morton, E.S. (1988). Song-type distribution in a population of Kentucky warblers. — *Wilson Bull.* 100, p. 9-16.
- Wiley, R.H. (1991). Associations of song properties with habitats for territorial oscine birds of eastern North America. — *Am. Nat.* 138, p. 973-993.
- & Richards, D.G. (1978). Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. — *Behav. Ecol. Sociobiol.* 3, p. 69-94.
- & — (1982). Adaptations for acoustic communication in birds: sound transmission and signal detection. — In: *Acoustic communication in birds*, Vol. 1 (D.E. Kroodsma & E.H. Miller, eds). Academic Press, New York, p. 131-181.
- Wilkinson, L. (1988). SYSTAT: the system for statistics. — SYSTAT, Evanston, Illinois.
- Williams, H. & Nottebohm, F. (1985). Auditory responses in avian vocal motor neurons: a motor theory for song perception in birds. — *Science* 229, p. 279-282.