RANGING BY SONG IN CAROLINA WRENS THRYOTHORUS LUDOVICIANUS: EFFECTS OF ENVIRONMENTAL ACOUSTICS AND STRENGTH OF SONG DEGRADATION

by

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Summary

Territorial male song birds most frequently hear conspecific song that has been degraded (distorted) by transmission through the environment. Their ability to use this accumulated degradation in conspecific song to assess the distance of its singer requires a receiver to discriminate between different degrees of degradation by taking into account the acoustical properties of the habitat. Ranging accurately when acoustical properties change seasonally then requires a receiver to reassess previous associations of degradation with distance.

Here I tested the possibility that Carolina wrens (*Thryothorus ludovicianus*) discriminate between different levels of song degradation and change their association of degradation with distance when the acoustical properties of their territories change. In response to playback of a single song, either undegraded or degraded (at two different levels), most subjects flew to the far side of the loudspeaker only in response to degraded songs. In addition, behavioral responses beyond the loudspeaker were consistently stronger to playback of degraded songs than to playback of undegraded songs. Responses indicate that wrens discriminated between different levels of degradation and suggest that they adjusted their association of degradation with distance as habitat conditions changed. Such adjustment of associating a given level of degradation with distance is an important requirement for accurate ranging, in particular under changing acoustical conditions of the environment. In addition, rapid ranging on the basis of only one song might facilitate processing of additional information such as

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a singers identity and motivation. Resulting selective attention to the closest rival might increase the reliability or speed of decoding such additional information.

Introduction

Several studies have shown that male territorial song birds can use the degradation of conspecific song during propagation through the environment to assess the distance of a singer (Richards, 1981a; McGregor *et al.*, 1983; McGregor & Falls, 1984; McGregor & Krebs, 1984; Shy & Morton, 1986; Naguib, 1995b; Wiley & Godard, 1996). This ability allows territory holders to discriminate between intruding rivals and distant conspecifics without spending time and energy approaching every singer. Estimating the distances of potential rivals then influences any further interaction among conspecific signalers and receivers, as the nature of their interactions strongly depends on their inter-individual distances. Thus, ranging plays a central role for vocal communication in song birds and in other animals with similar constraints on communication.

In order to accurately extract information from a song about the distance of its singer, a receiver needs to have some prior information about the structure of the song at its source or at about its level of degradation at different distances. In addition, a receiver will need to have some experience with the acoustical properties of its habitat. Combining this information will then allow a receiver to assess the length of a propagation path of a received signal.

When reverberation is used as a cue for auditory distance (Naguib, 1995b; Wiley & Godard, 1996), the receiver needs to take into account whether the propagation path contains few or many reflecting surfaces. Sound traveling over an open field does not accumulate much reverberation even over long distances (Michelsen, 1978; Wiley & Richards, 1978, 1982; Richards & Wiley, 1980). In contrast, dense vegetation in a forest causes sound to reverberate considerably, even over relatively short distances. Because reverberation strongly depends on the density of vegetation it increases after foliage has developed in spring (Richards & Wiley, 1980). A particular level of reverberation thus indicates a more distant bird before than after foliage has developed. Similar arguments apply to frequency-dependent attenuation. Although attenuation increases with frequency in all habitats, higher frequencies attenuate more rapidly in dense vegetation (Morton, 1975; Marten & Marler, 1977; Piercy *et al.*, 1977).

As a result criteria for associating degradation with distance should depend on the current acoustical properties of the habitat. A territory holder will be more effective in discriminating between intruders and distant conspecifics the better its ranging criteria are. However, direct evidence that birds take their habitat into account when judging the distance to conspecific singers is not available. Ranging experiments to date have focused either on ranging in general (Richards, 1981a; Fotheringham & Ratcliffe, 1995; Naguib, 1995b), on identification of particular cues (Naguib, 1995a; Wiley & Godard, 1996; Naguib, subm.), or on the role of familiarity with a song pattern (McGregor *et al.*, 1983; McGregor & Falls, 1984; McGregor & Krebs, 1984; Shy & Morton, 1986; Naguib, 1995a; Wiley & Godard, 1996). The underlying assumptions in these experiments are that territorial birds have acquired information about the acoustical properties of the habitat and are able to associate a song's degradation with its propagation distance.

This study investigated the possibility that Carolina wrens (*Thryothorus ludovicianus*) discriminate between different levels of degradation and change their ranging criteria with long-term changes in the acoustical properties of their territories. Because Carolina wrens defend territories throughout the year, often in deciduous forests, the acoustical properties of their habitat change in the course of the year. I simulated a conspecific rival with playbacks of undegraded and degraded songs in deciduous forests before and after foliage had developed. I predicted that subjects would respond differently at these two seasons to songs degraded at the same level.

As interpretations of ranging experiments are problematic when subjects gain close range experience with the loudspeaker, I used a playback design that allowed me to obtain direct evidence for misjudgments of the loudspeaker position (Naguib, 1996). By broadcasting only one song, either undegraded or degraded, about 30 m from a singing subject, I eliminated the subjects' opportunity to approach during playback and to use repeated cues to determine the location of the loudspeaker. I could thus obtain direct evidence for ranging by observing whether or not subjects flew beyond the loudspeaker.

Material and methods

General

I conducted this study from 13 March to 30 April 1994 in deciduous and mixed forests at the Mason Farm Biological Reserve at Chapel Hill, North Carolina, USA. These forests are dominated by several species of oaks and hickories (*Quercus*, *Carya*) 22-28 m tall with a dense understory of shrubs (*Virburnum rafinesquianum*), 1-1.5 m high (Wiley, 1977; Hall & Wiley, 1978). The experiment consisted of two parts. The first part was conducted from 13 to 26 March before foliage emerged. I then repeated the experiment with the same subjects and playback stimuli from 21 to 30 April after development of dense foliage. Eight color-banded male territorial Carolina wrens were used as subjects for playback experiments. Territory sizes (average 150 m in diameter) were assessed prior to the experiments by following movements of the subjects and by plotting song posts on a detailed map of the study area. All subjects remained on their territories from the beginning of the first part to the end of second part of the experiment. Although their reproductive state within the breeding season was not checked systematically, subjects were observed building nests in the first part of the experiment and presumably many were feeding nestlings in the second part of the experiment.

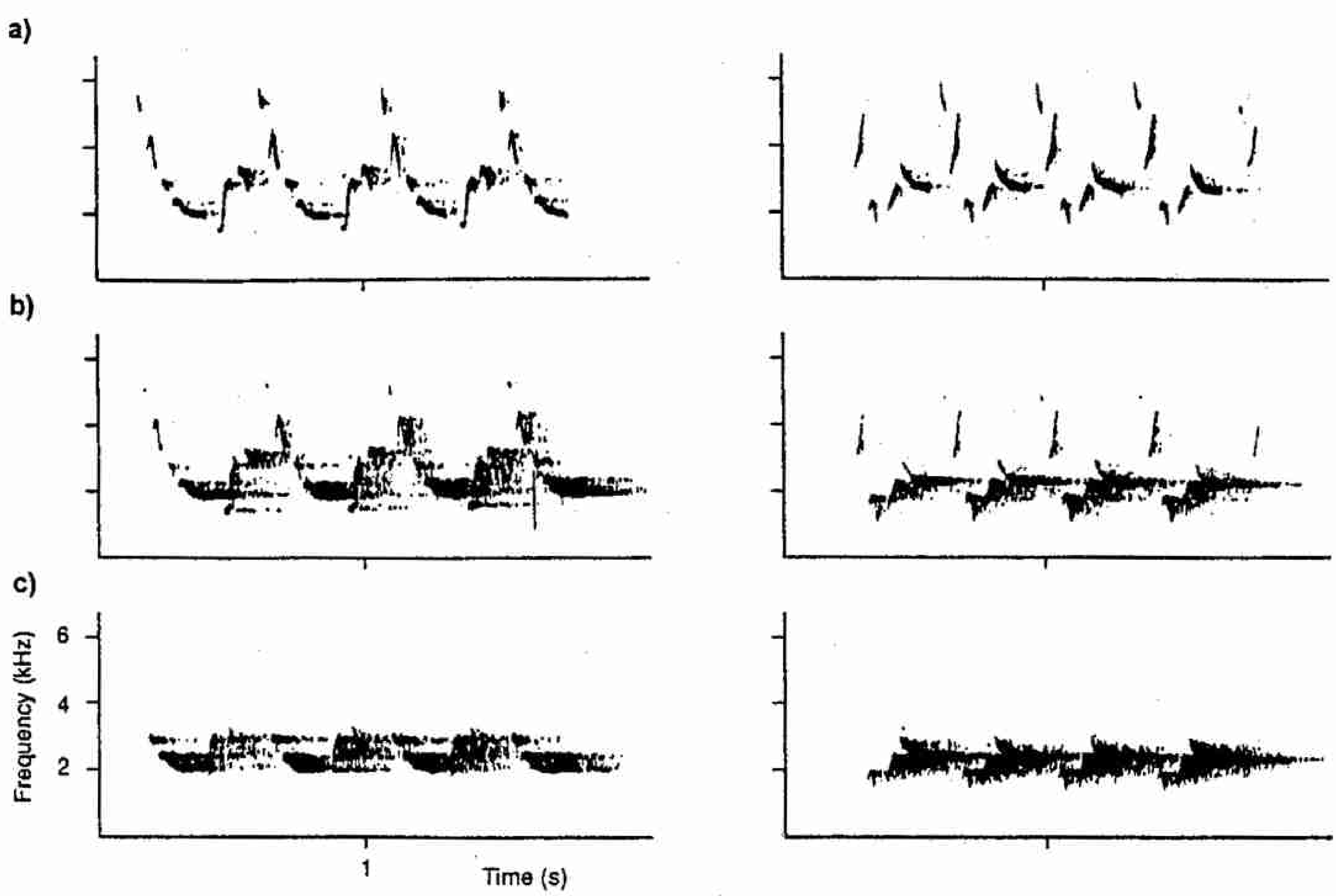

Fig. 1. Sound spectrograms of the three treatments of two song types: (a) undegraded, (b) less degraded, (c) more degraded.

Production of playback tapes

Playback tapes were produced from recordings made with a Sennheiser K3U/ME88 ultra-directional microphone and a Sony WM-D6C tape recorder within 6 m of male Carolina wrens in the study area in 1993. Four songs were selected after they had been checked for clarity on a real-time spectrum analyzer (Kay Electrics DSP Sona-Graph Model 5500). The songs were then digitized with 16-bit accuracy at 20 500 Hz on a Macintosh computer using Audiomedia software. Playback tapes of undegraded songs (D0) were produced by re-recording songs through a Krohn-Hite band-pass frequency filter (Model 3700, settings 1-10 kHz, Butterworth filter function, 24 dB/octave) on a Marantz PMD221 tape recorder. Degraded songs (D1 and D2, Fig. 1) were produced by reverberating and high-frequency attenuating the songs. Carolina wrens can use both cues for ranging (Naguib, 1995b). Reverberation was added by broadcasting the undegraded songs in a large attic from a Marantz PMD221 tape recorder connected to a Perma Power S-702 amplifier and a Realistic horn loudspeaker (frequency response 2-8 kHz ± 3 dB). The songs were recorded at 4 m (D1) and 9 m (D2), respectively, using a Sennheiser K3U/ME80 directional microphone and a Marantz PMD221 tape recorder. The attic (about 12 × 35 m) served as a reverberation chamber with no large parallel surfaces and many miscellaneous objects on the floor with multiple surfaces to reflect sound. This procedure had the advantage of creating complex reverberation without adding amplitude fluctuations or decreasing the signal-to-noise ratio as does broadcasting songs through a natural habitat and re-recording them at long distances. In order to assess the levels of reverberation I recorded 25 ms tone pulses (3 kHz) under the same conditions as degraded songs. To quantify the reverberation I integrated over the area of the reverberated tail of these pulses. The reverberation index, introduced by Richards & Wiley (1980), based on the 200 ms following a 25 ms pulse was within the range of those they measured for propagation ranges of 25 m in deciduous forest (Index for D1, 1.4; for D2, 1.7). The reverberation measured for less degraded songs was 86% of that measured for more degraded songs.

All songs were then digitized on a Macintosh computer using Audiomedia software. They were recorded on the Marantz PMD221 tape recorder through the band-pass filter mentioned above with pass bands of 1-5 kHz (D1) and 1-3 kHz (D2), respectively. Thus, more degraded songs (D2) had less energy in higher frequencies and also contained more reverberation than less degraded songs (D1).

Playback experiments

Within each of the two parts of the experiment, all eight subjects received three playback treatments at least 48 h apart in a balanced design. In order to control for possible influences of a particular song type on the responses I used four different song types, each in playbacks to two subjects. Subjects most likely had had prior auditory experience with the song types as they were all recorded in the study area. Neighboring Carolina wrens share 70-95% of their song repertoires (Simpson, 1982; Shy & Morton, 1986), and their loud songs can be heard over several hundred meters. However, no subject received playback of a song recorded from itself or a contiguous neighbor. Playback treatments consisted of one song, either undegraded (D0), less degraded (D1) or more degraded (D2) (Fig. 1) and were broadcast at 88 dB as measured at 1 m in a virtually anechoic environment. The song was broadcast about 30 m from the singing subject but at least 25 m within its territorial boundaries. For playback the horn loudspeaker mentioned above was clamped to a small tree about 1.8 m above ground and directed towards the singing subject. Songs were played from a Marantz PMD221 tape recorder through a Perma Power S-702 amplifier connected by a 10 m cable to the loudspeaker. The playback was only started when the contiguous neighbors were silent.

Responses were recorded for 45 min following the playback because Carolina wrens often have long latencies to respond actively and respond for a long time. The primary measure of response was approach, recorded in three categories: (I) approach within 20 m of the loudspeaker, as predicted for subjects that assessed its position more or less accurately, (II) flights to the far side of the loudspeaker, which clearly indicated over-estimation of the location of the loudspeaker (this behavior was expected for subjects estimating that the song came from within their territory but from a more distant position than the loudspeaker), (III) no approach within 20 m, as expected for subjects that ranged the song as coming from beyond the boundary. I tested the approach for statistical significance with a G-test (R $\times$ C test of independence with adjusted G-values; Sokal & Rohlf, 1987).

In addition, I measured (1) number of songs in the longest singing bout, (2) total number of songs, (3) number of songs on the far side of the loudspeaker, (4) percent of total number of songs on the far side of the loudspeaker, (5) time spent on the far side of the loudspeaker, (6) furthest distance subjects moved away from the loudspeaker on its far side, and (7) total approach distance (total distance that subjects moved from their original position towards (and beyond if applicable) the loudspeaker). High values for the first two measures of response reflected a generally high intensity of response as predicted for responses towards nearby intruders. High values for the latter five measures of response directly reflected an over-estimation of the loudspeaker position.

Since measures of all responses were correlated with each other to varying degrees ($r = 0.067$ to 0.89), I used a principal component analysis to extract one composite measure of response for each playback. The first principal component explained over 57% of the variance in responses and served as a measure of overall response for statistical analysis. The second component explained an additional 26% of variance.

Results

Approach

The majority of subjects moved beyond the loudspeaker in response to playback of degraded songs (Fig. 2a). In response to playback of undegraded songs, most subjects approached within 20 m of the loudspeaker without flying beyond it. About equal numbers of subjects did not approach the loudspeaker in response to any of the three playback treatments. The approach differed significantly among playback treatments ($G = 19.30$, $p < 0.001$, df $= 4$, G-test). These trends remained in comparisons of play-

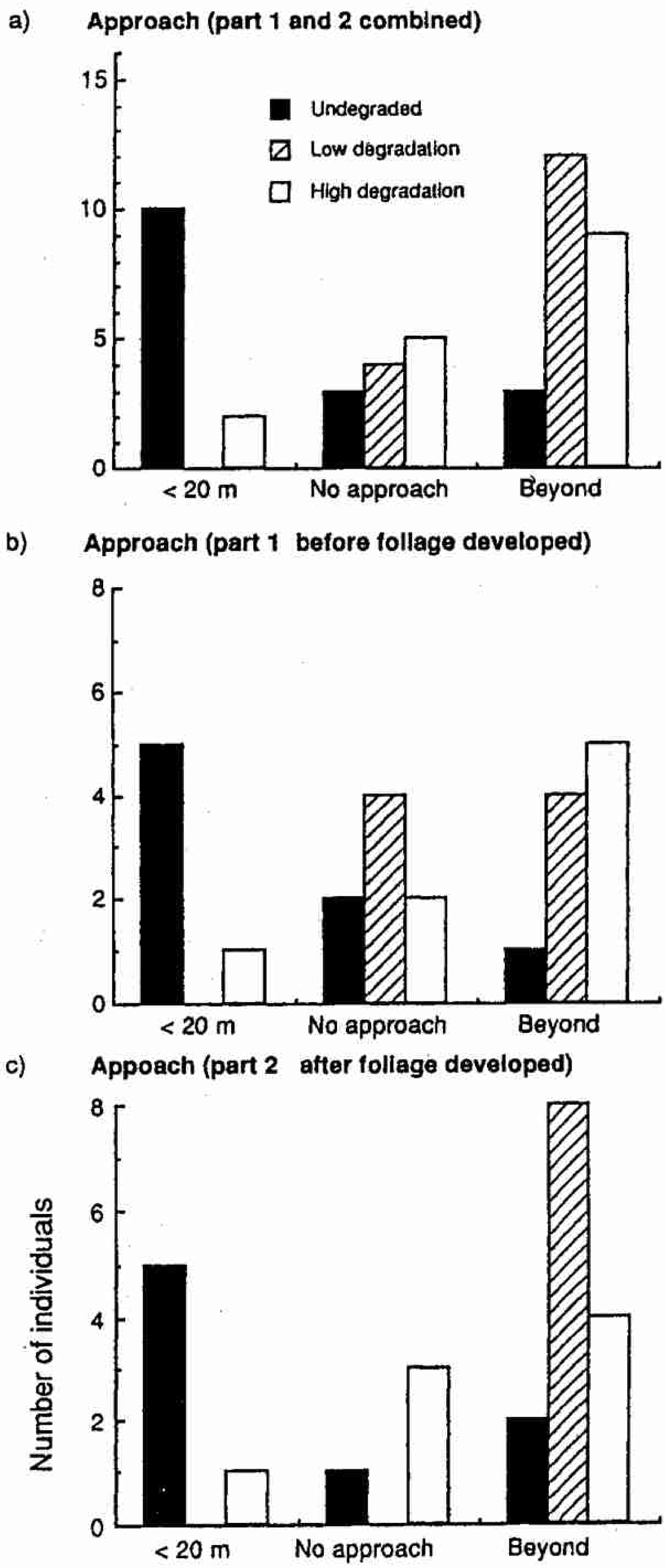

Fig. 2. Approach in response to playback of undegraded, less and more degraded songs: (a) both parts of the experiment combined, (b) before foliage had developed, (c) after foliage developed. The three categories of approach are approach within 20 m of the loudspeaker, no approach, and flying beyond the loudspeaker.

backs conducted before and after foliage had developed (before, $G = 10.64$, $p < 0.05$, df = 4; after, $G = 14.46$, $p < 0.01$, df = 4, G-test).

In response to playback of undegraded and more degraded songs, approaches were similar before and after foliage had developed, respectively (Fig. 2b, c; undegraded, $G = 0.30$, NS; more degraded, $G = 0.14$, NS, df = 2). Approaches to playback of less degraded songs, on the other hand, differed significantly from before to after foliage had developed, as more subjects flew beyond the loudspeaker after foliage had emerged ($G = 6.14$, $p < 0.05$, df = 2).

Thus, approaches directly indicated an over-estimation of distance of degraded songs in both parts of the experiment. Changes in approach between the two parts of the experiment were significant only for less degraded songs.

Additional response measures

Responses to different levels of degradation

Before foliage had developed subjects responded consistently differently to playback with increasing level of song degradation (Fig. 3a). Subjects' vocal responses in general were stronger to playback of undegraded songs than to playback of less and more degraded songs. In contrast, responses on the far side of the loudspeaker were consistently stronger to playback with more degradation (Fig. 3a). Also the mean distance that subjects moved away from the loudspeaker on its far side increased with increasing degradation.

Also after foliage had developed, subjects' vocal responses were more intense to playback of undegraded songs than to playback with either level of degradation (Fig. 3b). Mean responses on the far side of the loudspeaker were weakest to playbacks of undegraded songs and particularly intense to playbacks of less degraded songs. Unlike before foliage had developed, subjects now moved furthest away from their original position (towards and beyond the source of playback) to playback of less degraded songs. Responses beyond the loudspeaker to playback of more degraded songs were intermediate in this part of the experiment.

In summary, responses consistently indicated that subjects' over-estimated distance with increasing level of degradation before foliage had

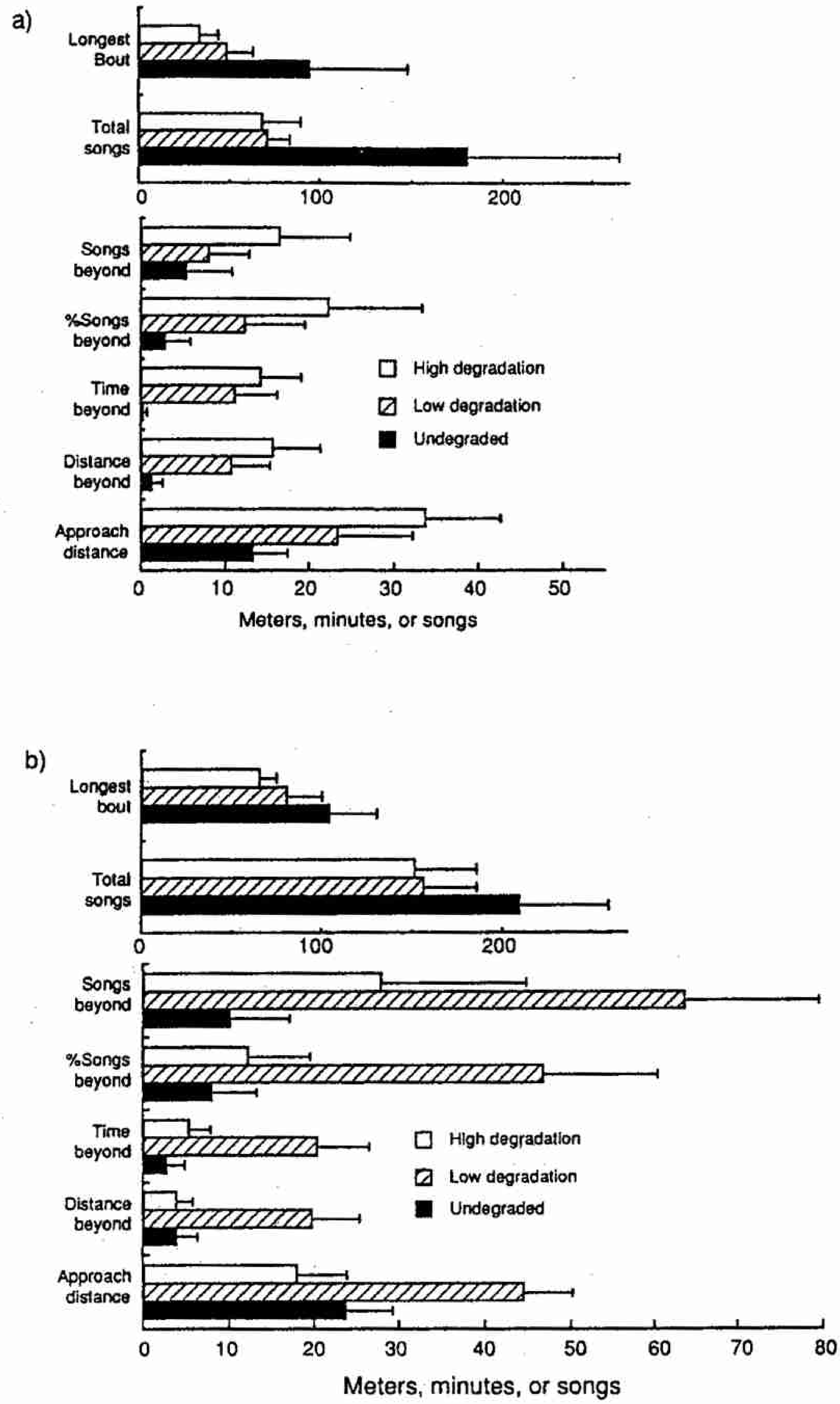

Fig. 3. Responses (± SE) of subjects to playback of undegraded, less and more degraded songs: (a) before foliage had developed and (b) after foliage had developed. *Longest bout*, number of songs in longest singing bout; *Total songs*, total number of songs; *songs beyond*, number of songs beyond the loudspeaker; *% songs beyond*, percentage of total songs beyond the loudspeaker; *time beyond*, time spend beyond the loudspeaker; *distance beyond*, furthest distance subjects over-flew the loudspeaker; *approach distance*, total distance that subjects moved from their original position towards (and beyond if applicable) the loudspeaker.

developed. After foliage had developed, behavior that directly indicated an over-estimation of distance was prominent only for less degraded songs.

Responses under acoustically different situations

In general, subjects tended to sing more in the second part of the experiment after foliage had developed (Fig. 3a, b). However, singing intensity in response to playback of undegraded songs did not differ as much before and after foliage had developed as it did to playback of degraded songs. Responses on the far side of the loudspeaker to playback of less degraded songs were considerably stronger in the second than in the first part of the experiment (Fig. 3a, b). Also subjects moved a much longer distance away from the original position after than before foliage had developed. In contrast, responses on the far side of the loudspeaker to playback of more degraded songs were in general stronger in the first than in the second part of the experiment (Fig. 3a, b).

Thus, a change in response with changes in the acoustical properties of the habitat was prominent only in playbacks of less degraded songs.

Composite measures of response (Principal component analysis)

Most response measures that loaded heavily on the first principal component involved behavior on the far side of the loudspeaker (Table 1). Thus, the scores on the first principal component primarily reflect differences in responses on the far side of the loudspeaker rather than the overall intensity

TABLE 1. *Loadings of the original response measures on the first two principal components (PC 1 and PC 2)*

	Components	
Response measures	PC 1	PC 2
Songs in longest singing bout	−0.374	0.877
Total number of songs	−0.283	0.940
Songs beyond the loudspeaker	0.761	0.333
Percent songs beyond the loudspeaker	0.884	0.210
Time beyond loudspeaker	0.878	0.068
Distance beyond the loudspeaker	0.906	0.046
Total distance of approach	0.901	0.077

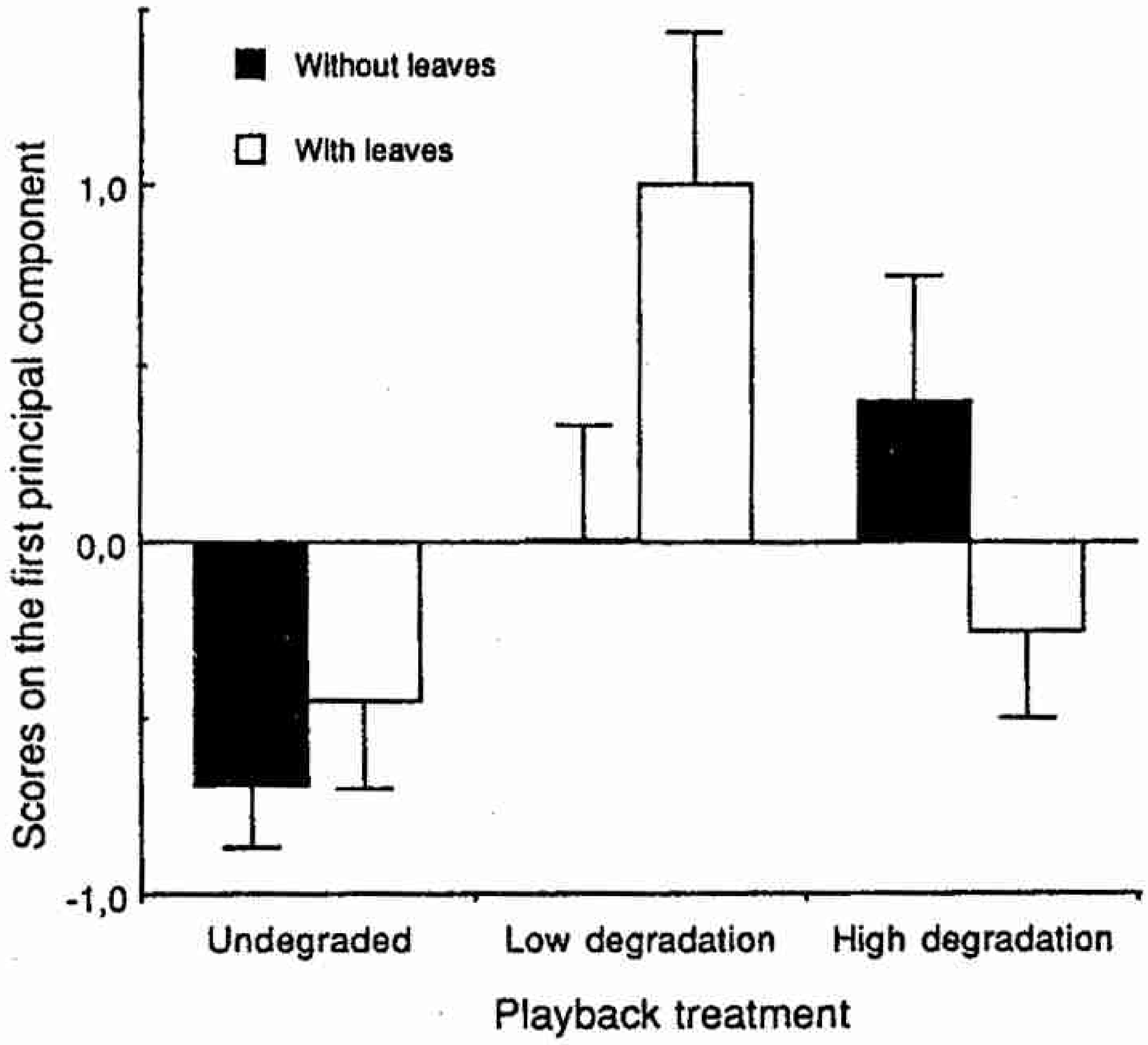

Fig. 4. Mean scores on the first principal component (± SE) separated by playback treatments.

TABLE 2. *Analysis of variance of the scores on the first principal component*

Source	df	*F*	*p*
Treatment	2	6.625	0.004
Time of playback (with and without foliage)	1	0.459	0.503
Song type	3	1.432	0.253
Subject	7	1.075	0.403
Order of playback	2	0.083	0.920
Treatment × Time	2	3.696	0.037

of response. An analysis of variance of the scores on the first principal component indicated a significant influence of playback treatment and of the interaction between treatment and time of experiment (before and after foliage had emerged) (Fig. 4, Table 2). Neither song type used for playback, subject, order of presentation of playback treatments, time of playback (before and after foliage had developed) had a significant influence on responses as measured by the first principal component (Table 2).

The regression of response scores (D0, D1, D2) indicated a significant change in response with increasing degradation before foliage had developed ($r = 0.94$, $p = 0.014$). After foliage had developed, this was not significant, as responses to more degraded songs were relatively weak. However, responses between undegraded and less degraded songs differed significantly ($p = 0.018$, Wilcoxon matched-pairs signed-ranks test).

Thus, the analysis of variance indicated that subjects responded differently to songs with different levels of degradation and that these differences were influenced by changes in the acoustical properties of the habitat. A consistent change in response with increase in degradation was evident in the experiment before foliage developed but not after foliage had developed.

Discussion

The results support prior findings that birds use the degradation of a song to estimate the distance of a singer (Richards, 1981a; McGregor *et al.*, 1983; McGregor & Falls, 1984; McGregor & Krebs, 1984; Naguib, 1995b; Wiley & Godard, 1996). Flights beyond the loudspeaker and intense responses on the far side of the loudspeaker primarily in response to playback of degraded songs provided unambiguous evidence for ranging. The responses also showed that Carolina wrens not only discriminate among undegraded and degraded songs, as shown earlier (Richards, 1981a; Morton *et al.*, 1986; Naguib, 1995b), but also among different levels of degradation under the same acoustic conditions. In addition, the changes in responses from before to after foliage had developed suggest that Carolina wrens changed their association of song degradation and propagation distance with these prominent changes in the acoustic properties of their territories.

One of the main problems in interpreting responses to playback of undegraded and degraded songs has been possible confounding influences. As recognized first by Richards (1981a) and acknowledged by all subsequent investigators (reviewed by Wiley & Godard, 1996), weak responses to playback of degraded songs can result from difficulties of detection or recognition and from habituation in addition to ranging. A new approach (Naguib, 1995a, 1996) similar to that of Wiley & Godard (1996) has reduced these ambiguities by eliminating subjects' close range experience with the loudspeaker and by measuring behavior that directly reflects over-estimations of the location of the loudspeaker. As in all prior experiments, the intensity of response in general was weaker to playback of degraded songs than to playback of undegraded songs. However, these differences in intensity of response were reversed on the far side of the loudspeaker. Strong responses on the far side of the loudspeaker are only predicted by influences of ranging and not by influences of detection, recognition, or habituation (Richards, 1981a; Wiley, 1994; Naguib, 1996; Wiley & Godard, 1996). The results thus provide strong evidence that the differences in behavior towards playback of undegraded and degraded songs in fact result from ranging.

Responses to different levels of degradation

The increasing strength of response on the far side of the loudspeaker with increasing degradation before foliage had developed indicated that subjects consistently judged more degraded songs as coming from farther away than less degraded and undegraded songs. The responses after foliage had developed can also be interpreted in this way but not as simply. In this case, responses to less degraded songs clearly indicated that subjects over-estimated the actual distance of the loudspeaker. Interpretation of responses to more degraded songs, however, is problematic although the weak responses beyond the loudspeaker could be the result of subjects estimating the song as coming from beyond the boundary. Less intense responses to playback of degraded songs were used as the prime evidence for ranging in earlier experiments (Richards, 1981a; McGregor *et al.*, 1983; McGregor & Falls, 1984; McGregor & Krebs, 1984; Shy & Morton, 1986; McGregor, 1994; Naguib, 1995b). However, as in these experiments, degradation could have influenced detection, recognition, and habituation. Thus, evidence for discrimination between different levels of degradation is unambiguous only for the part of the experiment conducted before foliage had developed.

Discrimination among different levels of degradation provides the basis for accurate ranging, as songs continuously accumulate degradation during their propagation through the environment. It is likely that birds can discriminate between even more levels of degradation, as such an ability would increase the accuracy of ranging and should be favored by natural selection. Accurate ranging would reduce the probability of making mistakes (Wiley, 1994) by approaching unnecessarily when no threat is at hand or by failing to approach when a rival in fact poses a threat. Nevertheless, variation in song degradation suggests that the value of discrimination on a very fine scale is limited. It is also possible that territorial song birds can range songs more accurately at the usual distance of territorial boundaries but less precisely on smaller or larger scales.

Responses under acoustically different conditions

The responses to playbacks before and after foliage had emerged suggest that subjects took into account the change in acoustical conditions when assessing the distance of the source of the song.

Undegraded songs evoked similar responses before and after foliage had developed, an indication that responses were not significantly influenced by motivational changes in the breeding season. Although the tendency for increased singing in the second part of the experiment presumably reflects motivational changes, these differences were not apparent in the measurements associated directly with estimation of the position of the loudspeaker. Instead, the similar responses to undegraded songs in both parts of the experiment suggest that subjects had adjusted their distance assessment to changes in the acoustical properties of their habitat. Compensation for changes in acoustic conditions would result in similar responses to playback of undegraded songs but not to songs that incorporate additional degradation, because a fixed level of added degradation reflects different propagation distances under different acoustical conditions.

The lack of approach by half the subjects in response to playback of less degraded songs before foliage had developed suggests that they judged these songs to come from beyond the boundary more often than they did after foliage had developed, when all subjects flew past the loudspeaker. Although it can not be ruled out that those subjects that did not approach failed to detect or recognize the playback, as discussed above, it seems unlikely that such influences were more prominent under the acoustically more favorable conditions before foliage had developed. Carolina wrens in fact do not approach songs that sound distant when such confounding problems can be ruled out (Naguib, subm.). Flights and strong responses beyond the loudspeaker by all subjects after foliage had developed indicated that subjects consistently over-estimated the propagation distance within the limits of the territory. These changes in behavior are presumably the result of receivers interpreting the same level of degradation in different ways, in accordance with the acoustical properties of the habitat. As songs degrade more rapidly after foliage develops (Richards & Wiley, 1980), these degraded songs were presumably perceived as coming from farther away before than after foliage had developed.

The similar responses to playback of more degraded songs in both parts of the experiment provide no direct evidence that subjects associated this level of degradation with different distances before and after foliage had developed. These relatively similar responses to more degraded songs could indicate that subjects judged the more degraded songs to come from beyond the boundary under both conditions. It is possible that territorial song birds do not discriminate levels of degradation beyond a certain level because a conspecific outside the subject's territory poses less of a threat than an intruder. Thus, even if the subjects ranged the more degraded songs differently under the acoustically different conditions, they might still have responded similarly because the simulated rival appeared to be too distant to be threatening under either condition.

Nevertheless, the similar responses to undegraded songs in combination with the changes in response to less degraded songs indicate that Carolina wrens took into account that songs degrade differently under different conditions. This result does not suggest that diverse habitat conditions hinder ranging (Fotheringham & Ratcliffe, 1995). Instead, compensation for at least seasonal changes in the acoustic conditions of a habitat seem to enable birds such as Carolina wrens to use their ranging abilities for efficiently defending a territory under acoustically varying conditions. Lack of such compensation would certainly result in inaccuracy of ranging by song degradation and consequently reduce the usefulness of ranging for defending a territory.

Implications for processing complex information

The differences in response to playbacks consisting of only one song show that birds have the ability to assess the distance of a potential rival quickly. The singers' distance is among the complex information transmitted by acoustic signals in addition to information such as species identity (Becker, 1982), individual identity and location (Richards, 1979; Falls, 1982; Godard, 1991; Stoddard *et al.*, 1991; Wiley *et al.*, 1991), intended receiver (Lemon *et al.*, 1981; Todt, 1981; Dabelsteen & Pedersen, 1993), and physiological states or motivation (Hultch & Todt, 1982; Schroeder & Wiley, 1983; Dabelsteen & Pedersen, 1990). Because of difficulties of decoding all information simultaneously with equal certainty receivers might initially attend to some information more than to others. In that case, the distance of a singer is most likely among the more crucial information because the evaluation of further information primarily depends on the distance and thus the threat of the potential rival. In other words, birds might become less attentive to a singer after they have determined that it is far away but become more attentive after they have determined that it is nearby. Identity and motivation of a rival is probably less important when it is far away but crucial when it is close. Using the first song in a bout to direct further attention is somewhat analogous to using the first notes within a song to increase attention to subsequent syllables (Richards, 1981b). Such alerting components as loud whistle-like notes in the first part of the song can increase the detection and recognition of subsequent parts of a song (Richards, 1981b) or call in frogs (Ryan *et al.*, 1990). These arguments might also apply to communication between the sexes, as in some species easily degradable acoustic structures are particularly important for females responding to male song (King *et al.*, 1981; Dabelsteen & Pedersen, 1990, 1993). Processing such subtleties of acoustic structure requires more attention, which could be enhanced by rapid ranging. Quickly assessing the distance to different signalers can not only speed up the decision how to react but also the decision towards whom any response should be directed. Thus, quick assessment of distance could play an important role in processing complex information in animal communication.

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Zusammenfassung

Territoriale Singvögel hören arteigenen Gesang meist nachdem sich dieser während seiner Ausbreitung durch das Habitat verändert (verfälscht) hat. Die Fähigkeit, die Entfernung singender Rivalen anhand dieser Veränderungen im Gesang abzuschätzen, setzt voraus, daß ein Empfänger mit den akustischen Eigenschaften seines Habitates vertraut ist. Eine genaue auditive Entfernungsabschätzung setzt ebenfalls voraus, daß ein Empfänger bei seiner Assoziation von Veränderungen im Gesang mit der Entfernung zum Sender saisonale Änderungen in den akustischen Eigenschaften des Habitates berücksichtigt.

Hier habe ich anhand von Vorspielexperimenten im Freiland untersucht, ob Carolina-Zaunkönige (*Thryothorus ludovicianus*) (1) zwischen Strophen mit verschiedenen Verfälschungsgraden unterscheiden und (2) in ihrer Assoziation von Gesangsverfälschung und Entfernung zum Sender saisonale Änderungen in den akustischen Eigenschaften ihres Habitates kompensieren. Durch Vorspiel von nur einer arteigenen Strophe konnten die Versuchstiere während ihrer Annäherung an den Lautsprecher keine weitere Erfahrung über seine genaue Position sammeln. Flüge am Lautsprecher vorbei nach Vorspiel von verfälschten Strophen zeigten eindeutig, daß solche Strophen als von weiterher kommend eingeschätzt wurden als unverfälschte Strophen. Starke Verhaltensreaktionen nach überfliegen des Lautsprechers, besonders nach Vorspiel von verfälschten Strophen, bestätigten dies. Die unterschiedlichen Reaktionen auf das Vorspiel von Strophen mit verschiedenen Verfälschungsgraden zeigen, daß Singvögel diese unterscheiden können. Reaktionsänderungen nachdem sich die Vegetation im Frühjahr verdichtet hatte, weisen darauf hin, daß die untersuchten Zaunkönige ihre Kriterien zur Entfernungsabschätzung zu einem gewissen Grade den jeweiligen akustischen Eigenschaften im Habitat anpassen können. Solche Kompensationen in der Assoziation von Signaländerung und Entfernung zum Sender sind eine wichtige Voraussetzung für ein genaues Abschätzen der Entfernung singender Rivalen unter sich ändernden akustischen Eigenschaften eines Habitates. Die schnelle auditive Abschätzung der Entfernung nach Vorspiel von nur einer Strophe könnte auch die Verarbeitung weiterer Information vereinfachen und beschleunigen. Eine resultierende selektive Aufmerksamkeit zu demjenigen Rivalen, der am nächstem ist, könnte dazu führen, bestimmte Informationen, wie Individualität und Motivation, schneller und zuverlässiger zu dekodieren.