

Auditory distance estimation in song birds: Implications, methodologies and perspectives¹

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Abstract

Acoustic signals such as bird song degrade progressively during atmospheric propagation and consequently provide information about the distance of the signaler. Information on the signaler's distance is particularly important for animals that use acoustic signals to defend a territory or, in general, to regulate their spacing. Male territorial song birds can use this information to assess the distance of a conspecific singer (called 'ranging'). This ability presumably increases the efficiency of defending a territory because it enables a territory holder to discriminate among threatening intruders and distant conspecifics without interrupting current behavior to, for instance, spend time and energy in approaching. There are a variety of factors that can influence the outcome of 'ranging experiments' of which some are discussed here. So far, playback experiments in the field that impeded close-range experience of subjects with the loudspeaker yielded the clearest evidence for ranging. Flights of subjects to positions beyond the loudspeaker in response to playback of degraded songs provide unambiguous evidence for over-estimation of distance of degraded songs and thus reduce problems of interpretation encountered in experiments that allow subjects' close-range experience with the loudspeaker. Furthermore, the accuracy of ranging can be influenced by the kind of degradation and the availability of song features that facilitate its assessment so that these factors, in addition to an appropriate playback design, should be taken into account in future experiments.

Keywords: Auditory distance estimation; Birdsong; Environmental acoustics; Playback experiments; Song degradation

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1. Introduction

The influence of progressive degradation of acoustic signals during atmospheric propagation from sender to receiver has received increasing interest in studies on vocal communication (e.g., Michelsen, 1978; Hansen, 1979; Wiley and Richards, 1978, 1982; Morton, 1982; Whitehead, 1987; Simmons, 1988; Wiley, 1991, 1994; Date and Lemon, 1993; McGregor, 1994; Naguib, 1995a,b). Acoustic signals attenuate and degrade progressively by reverberation, frequency-dependent attenuation and irregular amplitude fluctuations during transmission through the environment (Richards and Wiley, 1980; Wiley and Richards, 1978, 1982). Thus, in long-distance acoustic communication, receivers most often hear signals that are degraded to some degree. As all forms of degradation increase with propagation distance, they provide information about the distance of the signaler (Wiley and Richards, 1982). However, sound degradation is considerably influenced by constraints on propagation so that these potential cues to assess the distance of the signaler are not always equally available.

Assessment of auditory distance (called 'ranging') is particularly important for animals that use acoustic signals to regulate their spacing such as male birds that use songs to indicate the occupation of a territory. Thus, territory holders that can discriminate among distant rivals and nearby intruders without approaching can considerably increase the efficiency of defending their territory. Carolina wrens (*Thryothorus ludovicianus*), for instance, can use the overall amplitude, reverberation and the relative intensities of high frequencies as separate cues for ranging (Naguib, 1995a,b). Using several cues could increase the accuracy of ranging by pooling information acquired in different ways. In addition, it could enable receivers to range a signal under conditions in which not all cues are equally available.

Here, I will address some of the methodological problems encountered in ranging experiments, namely, experimental design, kind of degradation, and effects of familiarity with the song type on ranging.

2. Playback experiments

Studies on song birds take advantage of aggressive responses of territorial males to playback of conspecific song. Ranging experiments were traditionally conducted by broadcasting songs, either degraded or undegraded, for 1–3 min with the same intensity inside a subject's territory (review in McGregor, 1994). Degraded songs were produced prior to playback by broadcasting and re-recording undegraded songs over 50 to 200 m of the natural habitat. Aggressive responses of subjects approaching playbacks could then be measured in the vicinity of the loudspeaker. Less intense responses to playback of degraded songs were taken as evidence for ranging, as degraded songs indicate a distant and less threatening conspecific under natural conditions. Although different intensities of response to playback of degraded and undegraded songs partly reflect natural behavior towards distant and nearby conspecifics, interpretations remained problematic. Territorial song birds are usually spaced far apart and, thus, most frequently hear songs after degradation by transmission through the habitat. In contrast, they hear undegraded songs in rarer events of intruding rivals or boundary disputes with contiguous neighbors. Thus, territorial male song birds might be habituated to degraded songs and consequently not respond intensely to playback of such songs. In addition,

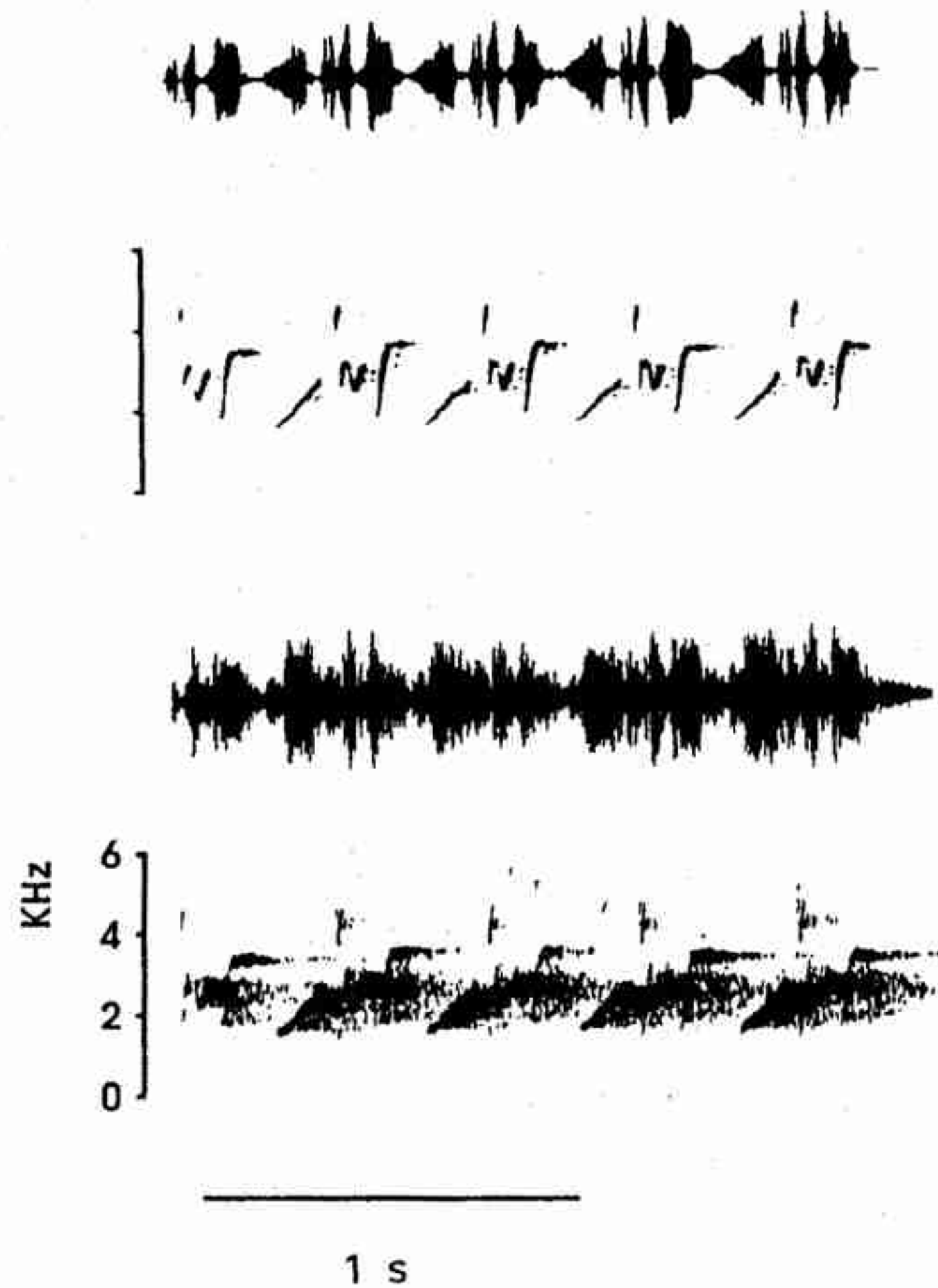


Fig. 1. Frequency spectrogram and waveform of a Carolina wren song type. (a) undegraded; (b) after artificial degradation, similar to propagation over 50 m of deciduous forest (details in Naguib, 1995a).

degradation increases problems of detection and recognition which could also cause less intense responses when degraded songs are used as playback stimuli (Richards, 1981; Wiley, 1994; Naguib, 1995a; Wiley and Godard, 1996).

Recent experiments which prevented subjects' close-range experience with the loudspeaker could considerably reduce such problems in interpreting responses (Naguib, 1995a, 1996; Wiley and Godard, 1996). Terminating playbacks before subjects approached closely yielded more direct evidence for ranging, as subjects flew to positions beyond the loudspeaker primarily in response to degraded songs. In experiments with Carolina wrens, for instance, playback treatments consisted of only one song, either clear or degraded (Fig. 1). Here, intensity of response in relation to the location of the loudspeaker was taken as evidence for ranging. Intensities of response on the far side of the loudspeaker were higher in playbacks of degraded songs than in playbacks of undegraded songs (Naguib, 1995a, 1996). Strong responses on the far side of the loudspeaker clearly indicate that subjects over-estimated the distance of the simulated rival. In addition, ranging a potential rival rapidly on the basis of one song is likely to speed up decisions how and towards whom to react and could be a mechanism to facilitate processing additional information in songs of more threatening rivals nearby. Thus, limiting subjects' close range experience with the loudspeaker provides a beneficial perspective not only for future ranging experiments but also for investigating whether other potential information such as singers' identity or motivation is decoded as quickly.

3. Familiarity with the song type

A second issue in ranging experiments is the degree of familiarity with the signal necessary to assess the degree of degradation. In order to assess the degradation of a signal, a receiver needs some information about the signals' characteristics at the source. As studies on song birds that addressed this issue have led in part to contradicting interpretations, the nature of this prior information remains unclear. Morton's ranging hypothesis (Morton, 1982, 1986) suggested, and some studies led to interpretations (McGregor and Falls, 1984; McGregor and Krebs, 1984; Shy and Morton, 1986a), that song birds need to know the particular song type for ranging. Other studies, however, indicated that song birds can also range unknown, novel song types (McGregor et al., 1983 (in part); Naguib, 1995a; Wiley and Godard, 1996). There could be a variety of reasons for these diverging interpretations (studies that found an influence of familiarity with the song type on ranging primarily relied on indirect evidence for ranging so that alternative interpretations of responses could not be ruled out reliably in all cases). However, here I want to focus on a less discussed aspect: the role that differences in song structure and song degradation play in ranging behavior.

Features that are important for assessing the degree of degradation are not necessarily equally present in all song types of a species. Prior knowledge that tonal frequency sweeps are present in all conspecific songs allows receivers to assess the degree of reverberation without knowing the particular song type (Naguib, 1995b). In Carolina wrens and Kentucky warblers (*Oporornis formosus*), for instance, all song types contain tonal frequency sweeps and males of these species can use reverberation to range even unknown song types (Naguib and Wiley, 1994; Naguib, 1995a; Wiley and Godard, 1996). Great tits (*Parus major*) and western meadowlarks (*Sturnella neglecta*), in contrast, discriminated among playback of clear and degraded songs only when they were familiar with the particular song type (McGregor and Falls, 1984; McGregor and Krebs, 1984). Although it could be argued that the responses in the latter studies, which allowed subjects' close-range experience with the loudspeaker, are confounded by other influences on responses, as discussed above, it is possible that familiarity with the song type plays a different role in the accuracy of ranging in different species, depending on variability between song types in that species. Thus, it may be possible that some species need more prior information about the song type for accurate ranging in particular when their song types differ considerably in characteristics that facilitate assessment of degradation. Although variation in the spectral composition among song types does not preclude ranging of unfamiliar song types (Naguib and Wiley, 1994; Naguib, 1995a), it may reduce the accuracy of ranging (on the basis of the relative intensities of high frequencies) when the frequency composition of the particular song type at its source is not known (Naguib, 1995b). Such problems might apply more to great tits than to Carolina wrens as great tits' song types cover a smaller frequency band than Carolina wren songs do so that effects of frequency-dependent attenuation in fact might be more difficult to assess in the former. In addition, in species such as great tits that do not include long tonal frequency sweeps in all songs, as Carolina wrens and Kentucky warblers do, accurate ranging of unfamiliar songs by reverberation also might be more difficult. Thus, some differences between studies might be dissolved when similarities among song types as well as the kind of degradation are taken into account.

Finally, quantifying degradation may help to some degree to compare signal degradation used in different experiments (Richards, 1981; Gish and Morton, 1981; Shy and Morton, 1986b; Dabelsteen et al., 1993; Naguib, 1996). However, such quantification can not eliminate one of the main handicaps

in ranging experiments in the field, such as the assessment of the songs' degradation at the actual position of the receiver during an experiment. It will be interesting to see if new and more sophisticated systems that can localize a singing subject passively (McGregor and Dabelsteen, 1996) can overcome these difficulties in field experiments.

In conclusion, ranging experiments can be improved considerably by using a playback design that eliminates close-range experience with the loudspeaker. Use of indirect evidence for ranging is presumably much of the source of diverging interpretations of ranging behavior. Investigations on the accuracy of ranging, however, might be limited eventually by the current rather coarse measurements of response and the problem of assessing the actual degradation of the playback stimuli at the receivers position during an experiment in the field.

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