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## Use of Song Amplitude for Ranging in Carolina Wrens, *Thryothorus ludovicianus*

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### Abstract

Songbirds are well known to use the degradation of conspecific song to assess the distance of the singer (called ranging). Because a song's degradation accumulates progressively with propagation distance and thus is not under direct control of the singer, it potentially provides more reliable distance information than the amplitude of songs. However, song amplitude decreases progressively with distance and thus also provides information about the singer's distance, provided that interference from wind is low and that the sender does not alter broadcast volume. This study investigated whether or not Carolina wrens, *Thryothorus ludovicianus*, can use changes in amplitude of conspecific song as a relative cue for ranging. Twelve male subjects each received one playback consisting of two successive songs differing by 6 dB in amplitude. Half the subjects received playbacks with the louder song first and the other half received playbacks with the louder song second. Receivers that would use song amplitude for ranging would perceive the simulated rival either as approaching or retreating, depending on whether the louder song was played first or second. Subjects responded as if the rival was farther away in the simulated retreat than in the simulated approach, indicating that Carolina wrens can use differences in amplitude of successive songs for ranging. Apparently, the risk of inaccurate ranging by song amplitude is outweighed by the advantage of using multiple cues, including information from song amplitude, to assess a rival's distance.

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### Introduction

For animals that use acoustic signals to regulate their spacing (WASER & WILEY 1979), auditory information about distances of signaling conspecifics, such as potential rivals or mates, is an important source of information. Long-range communication in territorial male songbirds is the best-studied example of the use of auditory information to assess the distances of conspecifics (called ranging, MCGREGOR 1994). In this case, ranging presumably increases the efficiency of defending a territory, because this ability allows territory holders to discriminate between distant and nearby rivals without spending time and energy in approaching.

Cues for ranging are provided by progressive attenuation and degradation (distortion) of acoustic signals during propagation through the environment (MORTON 1975; MICHELSEN 1978; WILEY & RICHARDS 1978, 1982). Because a signal's degradation is determined primarily by the properties of the transmission path rather than the sender's behaviour, it

potentially provides more reliable information for ranging than amplitude of a signal, which remains under the sender's control and depends considerably on wind conditions. Thus, all ranging experiments to date have studied the role of song degradation. These studies have shown that male territorial songbirds can range by song degradation (RICHARDS 1981a; MCGREGOR et al. 1983; MCGREGOR & FALLS 1984; MCGREGOR & KREBS 1984; MORTON & DERRICKSON 1996; NAGUIB 1996a, 1997; FOTHERINGHAM et al. 1997; but see FOTHERINGHAM & RATCLIFFE 1995) and that they can use either reverberation (NAGUIB 1995, 1997; WILEY & GODARD 1996) or the relative intensities of high frequencies (NAGUIB 1995, 1997) separately to range songs.

Although song amplitude is presumably not as reliable for ranging as these cues, it nevertheless provides information that could be incorporated in any distance assessment. In this case, however, a receiver would have to take into account wind conditions and sound shadows (WASER & WASER 1977; WILEY & RICHARDS 1978, 1982) which otherwise would limit accurate use of song amplitude for ranging. By using changes in song amplitude in successive songs, a receiver could reduce the uncertainties and would not need detailed information on absolute broadcast volume. Although senders that change broadcast amplitude or singing direction would confound ranging by song amplitude, birds often sing successive songs without noticeable changes in song amplitude, so that on many occasions amplitude could provide useful information for ranging.

It is important to emphasize that cues from degradation are also not fully reliable (DABELSTEEN et al. 1993; MATHEVON et al. 1996). In open habitats, for instance, reverberation will not provide reliable distance information. The information about distance provided by the relative intensities of high frequencies in a signal also has limitations. Because high frequencies are inevitably broadcast with more directionality than low frequencies (WITKIN 1977; LARSEN & DABELSTEEN 1990), it could be difficult for a receiver to decide on a fine scale whether a perceived reduction in high frequencies in a song is due to a change in the singer's distance or to a change in the direction a singer faces. Thus, despite some uncertainties, birds might benefit from including song amplitude in the suite of cues used to assess the distance of singing conspecifics.

This study investigated whether or not Carolina wrens, *Thryothorus ludovicianus*, use changes in amplitude of successive songs to assess changes in the distance of a singing rival. I simulated a rival by playing two successive songs with either the first or second song louder by 6 dB. Subjects that would use differences in amplitude of songs for ranging would perceive the treatment with the louder song first as a retreating rival and the treatment with the louder song second as an approaching rival. Such short playbacks have the advantage that they minimize the possibility that subjects approach during playback, thus preventing them from localizing the position of the loudspeaker (NAGUIB 1996a).

## Material and Methods

### General

The study was conducted at the Mason Farm Biological Reserve at Chapel Hill, North Carolina, USA. Twelve territorial male Carolina wrens were used as subjects for playback experiments from May 3 to May 7, 1994. Subjects held territories in mature mixed and deciduous forests, dominated by several species of oaks and hickories 22–28 m tall, mostly with dense shrubs in the understory, 1–1.5 m high. Territories were estimated

by following movements of subjects and by plotting their singing locations on a detailed map in almost daily visits to the study area during the 2 mo prior to the experiments. All subjects had mates and, although their stage in the breeding cycle was not checked systematically, observations suggested that most subjects were feeding nestlings.

### Production of Playback Tapes

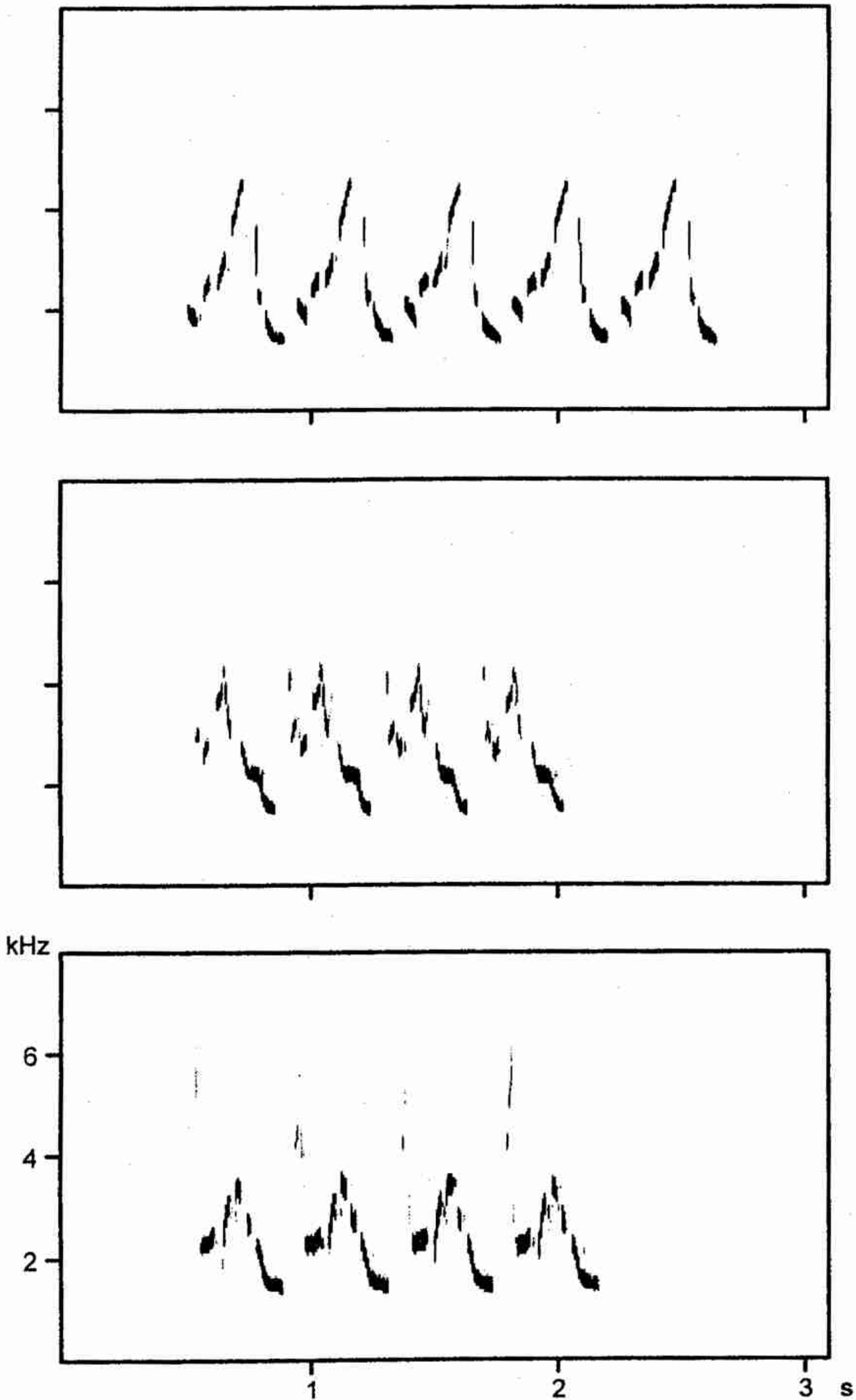
Songs used for playback were recorded with a Sennheiser K3U/ME88 directional microphone and a Marantz PMD221 tape recorder within 3–6 m of colour-banded Carolina wrens in the study area in spring 1993 (Fig. 1). Subjects most likely were familiar with these song types, as neighbouring Carolina wrens share about 70–95% of their song repertoires (SIMPSON 1985; SHY & MORTON 1986), and songs can be heard over at least two territories. However, no songs used for playback were recorded from the subject or its contiguous neighbours. To control for possible influences of a particular song type, I used songs of three different types for playback and presented each to four separate subjects. Songs were checked for clarity with a real-time spectrum analyser (Kay Electrics DSP Sona-Graph Model 5500) and digitized with 16-bit precision at a sampling rate of 20.5 kHz on a Macintosh computer using Audiomedia software. One copy of each song type was then reduced in amplitude by 6 dB using Audiomedia. A difference in 6 dB corresponds to doubling or halving of propagation distance with spherical spread of the sound wave and no excess attenuation. In reality, however, a change by 6 dB corresponds to a smaller change in distance as a result of excess attenuation of about  $10 \pm 5$  dB/100 m in the frequency range of Carolina wren songs (MORTON 1975; MARTEN & MARLER 1977). If subjects could use changes in song amplitude for ranging, these playbacks would then provide conflicting messages as song degradation was the same in both treatments. This situation arises in all behavioural experiments in which one of several cues is manipulated. To investigate use of particular cues for ranging, a first step is to emphasize the cue in question (NAGUIB 1995).

All songs were then re-recorded on a Marantz PMD221 tape recorder with the record level in a constant position. Two tapes for playback were prepared for each song type. Each tape contained two songs, one tape with the louder song first (simulated retreat) and one tape with the louder song second (simulated approach). The two songs on each tape were separated by a silent interval of 3 s, a natural rate of singing in Carolina wrens. Carolina wrens in the study population were often observed to sing such short bouts within the 3 yr I studied that population so that the short playback reflected naturally occurring song performance. This short playback also reduced the receivers' opportunity to obtain close-range experience with the loudspeaker. By reducing the possibility that subjects locate the loudspeaker by approaching during playback, experiments can provide direct evidence for ranging (NAGUIB 1996a,b; WILEY & GODARD 1996).

### Playback

Playbacks were broadcast between 0600 and 0900 h, after termination of the dawn chorus. The loudspeaker was placed about 25 m from a subject and at least 20 m within the boundary. The playback started when the subject was singing and when contiguous neighbours were silent. Although wind speed was not measured, it was low in all trials. For playback, I used a Marantz PMD221 tape recorder connected to a Perma Power S-702 amplifier and a Realistic horn loudspeaker (frequency response, 2–8 kHz  $\pm$  3 dB) clamped to a small tree about 2 m above ground. Six subjects received playbacks with the louder song first, and six subjects received playbacks with the louder song second. The amplifier gain was adjusted to make the louder song in each trial 88 dB at 1 m, as determined with a Realistic sound level meter 2 m above ground in a virtually anechoic environment, above vegetation 1 m deep in the centre of a large field. These measurements also confirmed the 6 dB difference between the two identical songs on each tape.

Responses were recorded for 30 min following playback. Contiguous neighbours on the side of the territory from which playbacks were conducted remained silent during this period in all trials. Because all measures of response (see below) were correlated ( $r = 0.12$ – $0.99$ ), I used a principal component analysis to extract one composite measure of response for each playback (MCGREGOR 1992). The scores on the first principal component were then used for statistical analysis. The first component explained 58% and the second component an additional 29% of variance in the data. The response measures and their respective loadings were number of songs,  $-0.584$ ; longest singing bout,  $-0.677$ ; number of song types,  $-0.620$ ; time spent beyond loudspeaker,  $0.857$ ; number of songs beyond loudspeaker,  $0.869$ ; percentage of songs beyond loudspeaker,  $0.885$ ; approach distance (closest approach of subjects that did not fly beyond the loudspeaker and distance subjects moved away from the loudspeaker on its far side for those subjects that over-flew the loudspeaker),  $0.772$ . The latter four



*Fig. 1:* Sound spectrograms of song types used for playback

measures of response, for which high values indicate an over-estimation of distance, loaded positively on the first principal component. The first three measures of response, for which high values indicated a strong response in general (SIMPSON 1985; NAGUIB 1995), loaded negatively on the first principal component. Because most response measures were associated directly with overestimation of distance, scores on the first principal component do not only indicate response intensity in general, but instead primarily indicate differences in response with regard to the location of the loudspeaker.

## Results

All responses differed in comparison of playbacks with the louder song first and those with the louder song second (Fig. 2). In response to playbacks with the louder song first, one subject approached closely, two subjects did not approach, and three subjects moved to positions beyond the loudspeaker. Movements to positions beyond the loudspeaker were straight flights, in two cases as far as 25 m beyond the loudspeaker's location. In response to playbacks with the louder song second, four subjects approached within 10 m of the loudspeaker, and two subjects moved beyond the loudspeaker, but less than 5 m.

The three measures indicating a generally higher intensity of response (number of songs, longest singing bout, and number of song types) were stronger in playbacks with the louder song second than in playbacks with the louder song first (Fig. 2). In contrast, responses reflecting more intense activity beyond the loudspeaker (time spent beyond the

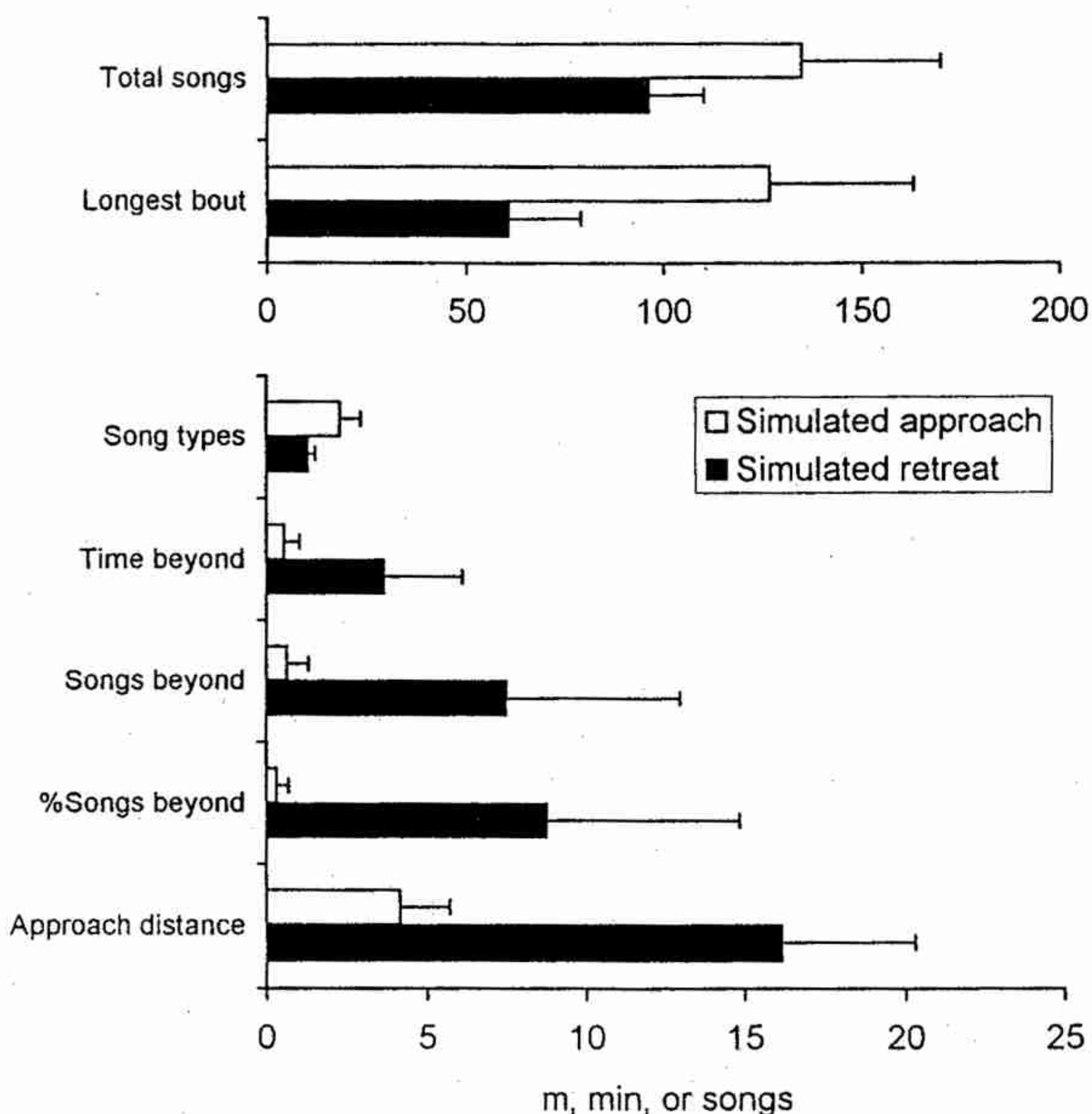


Fig. 2: Means ( $\pm$  SE) of original response measures. Total songs: total number of songs; longest bout: number of songs in the longest singing bout; song types: number of song types; time beyond: time spent beyond the loudspeaker; songs beyond: number of songs beyond the loudspeaker; % songs beyond: percentage of total songs beyond the loudspeaker; approach distance: closest approach for subjects that did not fly beyond the loudspeaker and, for those subjects that over-flew the loudspeaker, the distance they moved away from it on its far side

loudspeaker, number of songs and percentage of songs beyond the loudspeaker) were consistently stronger in response to playbacks with the louder song first than in playbacks with the louder song second. In addition, clear differences in approach distance suggest that subjects estimated the location of the rival as farther away when the louder song was first than when it was second. The scores on the first principal component, as a combined measure of response, indicate that subjects responded significantly differently to playback with the louder song first than to playback with the louder song second ( $p = 0.026$ , Mann—Whitney U-test, two tailed).

## Discussion

### General

Can Carolina wrens use changes in amplitude of successive songs as a cue for ranging? Receivers that use changes in song amplitude for ranging would perceive an increase in amplitude over successive songs as an approaching rival and a decrease in amplitude over successive songs as a retreating rival. Subjects responded more intensely to playbacks with an increase in amplitude. However, responses behind the loudspeaker were reversed: behind the loudspeaker, subjects responded most intensely to playbacks with a decrease in amplitude over successive songs.

The generally more intense response to playbacks with the louder song second could indicate either that subjects perceived the increase in amplitude over successive songs as a more aggressive intruder (MORTON 1982) without regard to its distance, or that they perceived the simulated rival as having approached during the silent interval between songs. Although the first possibility may well have influenced the general intensity of response, the subjects' approach behaviour and more intense response behind the loudspeaker in playbacks with the louder song first suggest that they in fact ranged the simulated rival differently in these two situations. Alternatively, it is possible that subjects did not attend to the difference in amplitude between songs, but instead were alerted by the first song and then primarily used information for ranging from the degradation of the second song. Thus, in those trials in which the second song was louder, subjects approached the loudspeaker more closely, because they were better able to assess degradation when the song was louder. In those trials in which the second song was less loud, according to this alternative, they were less accurate in assessing degradation and thus either did not approach and rather waited for information from further songs or moved straight to their territorial boundary to advertise it. Although this possibility could have contributed to subjects' responses, the results nevertheless suggest that subjects ranged the simulated rivals differently in both treatments. Firstly, subjects should have been alerted by the first song in both playback treatments, and even more so when the louder song was first (RICHARDS 1981b; WILEY 1994), so that it appears unlikely that they were unable to range the second song in those trials in which it was less loud. More importantly, previous findings have shown that one song is sufficient for ranging in Carolina wrens (NAGUIB 1996a). These considerations thus suggest that subjects took into account differences in amplitudes of both songs and perceived playbacks with the louder song first as a retreating rival and playbacks with the louder song second as an approaching rival.

### Implications of Ranging by Comparison of Song Intensities

Ranging by song amplitude is potentially less reliable than ranging by song degradation, and it has been argued that receivers should be less likely to use this cue for ranging (WILEY & RICHARDS 1978; RICHARDS 1981a; MORTON 1982; MCGREGOR et al. 1983; MCGREGOR & FALLS 1984; SHY & MORTON 1986; MCGREGOR 1994; FOTHERINGHAM & RATCLIFFE 1995; NAGUIB 1995, 1996a; WILEY & GODARD 1996). This experiment, however, suggests that Carolina wrens attend to differences in amplitude of successive songs at least for judging changes in a rival's positions. Humans also use the amplitude of a signal in addition to its degradation as a relative cue, and less accurately as an absolute cue, to assess the distance of a sound source (MERSHON & KING 1975; STRYBEL & PERROTT 1985). Even if songbirds also cannot accurately judge absolute distance of conspecifics by absolute amplitude of songs, attending to differences in song amplitude allows them to monitor movements of conspecifics and thus allows them to assess differences in distances of different signallers (MCGREGOR & DABELSTEEN 1996). Such movements of conspecifics, in particular with regard to territorial boundaries, are crucial for the subsequent behaviour for a male defending its territory. Furthermore, assessing relative distance has the advantage that use of amplitude for ranging does not fully depend on broadcast volume, which can differ between individuals and situations (SIMPSON 1985). These arguments hold in particular in calm weather when wind conditions hardly interfere with song amplitude. Under windy conditions, ranging by amplitude might be so ambiguous that birds attend more to reverberation or the relative intensities of high frequencies (NAGUIB 1995).

Nevertheless, even under the most favourable acoustic conditions, there remains the problem that a sender can change song amplitude and thus interfere with a receiver's mechanisms of ranging. Even if songbirds would benefit by doing so, as suggested by MORTON (1982, 1996), they may not do so on all occasions. Long-term neighbours, such as resident Carolina wrens, for instance, might develop mutualistic, rather than deceptive relationships for singing (GODARD 1993). If so, it might not be advantageous to provide receivers with misleading information. However, when circumstances might favour deception, perhaps during boundary disputes or during establishment of a territory, receivers might avoid including information from song amplitude in their assessment of a rival's distance.

### Integration of Cues for Ranging

Responses of Carolina wrens to playbacks suggest that they attend not only to a song's degradation but also to changes in amplitude of songs for ranging. To reduce the probability of making mistakes by using information from song amplitude for ranging, receivers conditionally might avoid using such information, as discussed above. They might use amplitude for ranging, for instance, primarily in favourable weather and situations in which they are not immediately involved in aggressive interactions such as in boundary disputes or during establishment of a territory. This possibility would require a conditional preference for some cues over others, as in visual depth perception in humans (DAVIES & GREEN 1994) and in orientation of migratory birds (WILTSCHKO & WILTSCHKO 1994). As information of the clear changes in amplitude apparently was weighted more

than the information from song degradation, it appears that not all cues are valued equally. It would be interesting to know how the information from different cues is incorporated in the final judgment. In any case, incorporating information from multiple cues could considerably reduce the different kinds of uncertainties associated with each cue and thus could increase the accuracy of ranging.

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