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Duplex auditory distance assessment in a small passerine bird (*Pipilo erythrophthalmus*)

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Abstract Eastern towhees, *Pipilo erythrophthalmus*, (Emberizidae, Passeriformes) in Florida estimate source sound-pressure level (SPL; i.e., sound amplitude) and often misjudge speaker distance in the field when vocalization source SPL is varied experimentally. Sound frequencies below ~3.5 kHz attenuate reliably with distance in comparison with higher sound frequencies in Florida scrub habitat. As a result, I predicted that towhees should use SPL as an auditory distance cue when they hear stimuli produced with sound frequencies below ~3.5 kHz but use another cue when they hear stimuli produced with sound frequencies above ~3.5 kHz. Subjects often misjudged speaker distance when approaching playbacks of SPL-altered stimuli produced with sound frequencies below ~3.5 kHz but rarely misjudged speaker distance when played SPL-altered stimuli produced with sound frequencies above ~3.5 kHz. I discuss the possibility that towhees employ a duplex sound localization strategy.

Keywords Auditory distance · Eastern towhee · Passerine bird · Ranging · Sound localization

Introduction

Accurate sound source localization can play an important role in mediating physical and social interactions across territory boundaries by allowing defenders to track or survey locations of mates or rival conspecifics. In addition, sound localization can often play a critical role in interactions with other species (e.g., predator localization or evasion and prey localization) and can improve signal detection in noisy natural environments (Klump 1996; Dent et al. 1997).

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Eastern towhees, *Pipilo erythrophthalmus* (Emberizidae, Passeriformes), are highly territorial and will often fly with surprisingly little error to the location of a small camouflaged speaker after a call stimulus has been played (Nelson and Stoddard 1998). Subjects ignore inactive speakers located near this active speaker and, as a result, the distance flown from a starting perch towards this playback speaker can be used to directly quantify auditory distance assessment in this species.

Eastern towhee calls are highly variable in acoustic structure. However, analyses of calls produced by caged subjects in the field demonstrate that several sound frequency variables and call duration are strongly correlated with calibrated measurements of source sound-pressure level (SPL, i.e., sound amplitude, Nelson 2000). These correlations may exist for several reasons but are critical to an investigation of auditory distance assessment because they allow for an estimation of source SPL in recorded calls (Nelson and Stoddard 1998). These correlations are also important because they allow for the manipulation of source SPL independently of spectral and temporal variables and the direct investigation of SPL as an auditory distance cue (Nelson 2000).

Towhees also appear to estimate source SPL using at least one correlated sound frequency or temporal variable and appear to judge auditory distance using the difference between perceived (incident) SPL and source SPL (Nelson 2000). That is, subjects appear to estimate source SPL and then use attenuation of SPL over distance as a cue. Nevertheless, towhee subjects do not always use SPL and are often able to assess distance accurately despite experimental variation of source SPL (Nelson 2000) or the imposition of degradation (Nelson and Stoddard 1998). As a result, towhees appear to use at least one additional auditory distance cue that has yet to be identified experimentally.

Frequency dependent attenuation (i.e., greater attenuation of high sound frequencies relative to lower sound frequencies) and degradation are auditory distance cues that appear to be used by other avian species (e.g., Richards 1981; McGregor and Falls 1984; McGregor

and Krebs 1984; Shy and Morton 1986; Naguib 1995; Morton and Derrickson 1996; Wiley and Godard 1996; Fotheringham et al. 1997; Naguib et al. 2000). Nevertheless, Nelson and Stoddard (1998) suggested that towhees in Florida scrub habitat use neither degradation that is reproduced from a single playback speaker nor frequency dependent attenuation as auditory distance cues.

Animals communicating over distance should use the auditory distance cue that is most reliable, on average, over time and throughout the local habitat. Alternatively, animals may use more than one auditory distance cue if individual cue reliability varies: (1) over time, (2) throughout the local habitat, (3) as a function of signaler or listener elevation, or (4) as a function of a vocalization (sound) variable.

Sound frequencies below ~ 3.5 kHz attenuate more reliably over distance in Florida scrub habitat than higher sound frequencies (Nelson, submitted). That is, sound frequencies below ~ 3.5 kHz often propagate through Florida scrub habitat with less variation in attenuation as a function of speaker elevation, microphone elevation and recording site. These results suggest that when towhees assess distance to playbacks of stimuli produced with sound frequencies below ~ 3.5 kHz they should use SPL as an auditory distance cue. In addition, these results suggest that towhees should rely on a second, as of yet unidentified, cue if this second cue correlates more reliably with distance over higher sound frequencies. I test these predictions by measuring the distances subjects fly in response to experimentally amplified or attenuated stimuli produced with sound frequencies either above or below ~ 3.5 kHz and discuss the possibility that towhees employ a duplex sound localization strategy.

Methods

Subjects

I selected 25 male eastern towhees as subjects in 1998 and 18 in 1999, choosing birds that frequented a conspicuous perch near their territory boundary that could be used as a starting perch during playback trials. All subjects defended territories in a scrubby flatwoods or sand pine scrub vegetation association (Abrahamson et al. 1984) and the defended territories that I selected were always separated by at least two additional territories that were defended by untested subjects. Towhees are often wary after being captured and, therefore, I did not color-band subjects in 1998 or in 1999 so that flights in response to playbacks would be biased minimally by my presence. Towhee subjects can be identified reliably on their territories during a single year and often keep the same territory from year to year (personal observations). Different territories were tested each year and it was my impression that subjects tested in 1998 were not again tested in 1999. All aspects of this study were conducted at Archbold Biological Station, 12 km south of Lake Placid, Florida, USA.

Production of sound stimuli

In both 1998 and 1999, I synthesized a single whole-call stimulus with sound frequency and temporal variables appropriate for a call produced with an 80-dB source SPL as predicted by correlations with RMS SPL (Nelson 2000; time, frequency and RMS SPL cal-

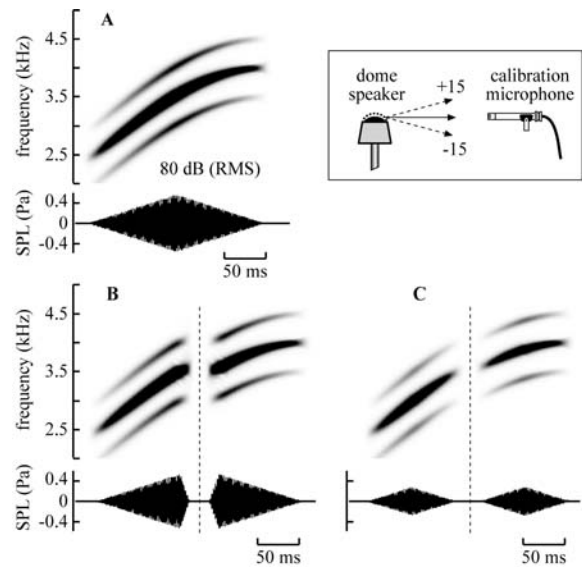


Fig. 1A–C Time-frequency spectra and time-amplitude waveforms of synthetic towhee call stimuli used in field playback experiments. **A** Whole-call stimulus spanning sound frequencies to each side of 3.5 kHz. **B** 1998 experimental stimuli produced with unequal onset and termination envelopes and with sound frequencies either above or below 3.5 kHz. **C** 1999 experimental stimuli produced with equal onset and termination envelopes and with sound frequencies either above or below 3.5 kHz. *Inset* Orientation of the playback speaker with respect to the elevation of the microphone used to calibrate source SPL

culated from calls recorded at a distance of 100 ± 10 cm with acoustic foam absorbing reflections from the ground). I used an 80-dB call stimulus because, on average, calls produced with an 80-dB source SPL sweep upwards to 3.5 kHz at 50% of overall call duration (Fig. 1; Nelson 2000). This 80-dB stimulus was produced digitally with 16 bits/sample, 210-ms duration, 2.4-kHz carrier frequency, 1.6-kHz deviation frequency, and 1.1-kHz sinusoidal modulation frequency. A 16-bit synthetic stimulus has a dynamic range that is greater than can be obtained when a vocalization is recorded in the field (-98 dB theoretical vs ~ -50 dB typical at a distance of 100 ± 10 cm). In addition, spectral and temporal measurements are typically obtained from vocalizations only above a predetermined threshold spectrum level. As a result, frequency modulation (FM) in this call is best described using a sine function $\{FM = 2.678 + 1.317[\sin(8.5x - 0.12)]\}$; arguments given in radians, x = time in seconds; measurements obtained above a 17-dB spectrum level threshold, 4,096 point FFT, equivalent to a 50-dB RMS threshold.

Amplitude modulation (AM) with a frequency (rate) of 500 Hz and depth of 20% was produced in each call by summing ± 500 Hz, -20 -dB side-bands together with the carrier just described. I enveloped this whole-call stimulus using a triangular envelope with a maximum SPL at 50% of call duration, or using one of the 1998 or 1999 half-call experimental envelopes described below (Fig. 1). I copied the three stimuli produced in each year and altered their amplitudes digitally to produce a total of six stimuli in 1998 and a total of nine stimuli in 1999 (-6 dB in 1998 and ± 6 dB in 1999). In all cases, RMS SPL values are referenced to 20 μ Pa and a 50 dB RMS threshold was used to define the selection over which RMS SPL was measured.

I used synthetic call stimuli, as opposed to previously recorded (and experimentally manipulated) 80-dB calls, to place an emphasis on defined spectral and temporal variables (Nelson 2000). In addition, I used synthetic stimuli to avoid subtle intracall variation that might convey additional information. Only a single stimulus was used to derive all stimuli because only a sin-

gle exemplar stimulus can be generated with spectral and temporal variables appropriate for a call produced with an 80-dB source SPL.

Towhee calls with an 80-dB source SPL normally reach a peak SPL near 65% of overall call duration. However, in this study, I applied a triangular envelope with a maximum SPL located at 50% of overall call duration. Use of this envelope allowed me to produce two experimental half-call stimuli with identical SPL and duration spanning sound frequencies either above or below 3.5 kHz (Fig. 1).

Towhees in Florida do not normally produce calls with sound frequencies only above 3.5 kHz and, as a result, I could not conduct this playback experiment using whole-call stimuli. In addition, because call source SPL is correlated strongly with several spectral and temporal variables (Nelson 2000), playbacks of variable whole-call stimuli would increase the number of potentially confounding variables involved and the number of control stimuli required.

In 1998, I produced half-call experimental stimuli spanning sound frequencies to each side of 3.5 kHz using triangular envelopes with either rapid onset or termination times (5.25 ms, Fig. 1B), and with overall duration equal to 52.5% of the control stimulus's overall duration (Fig. 1B). I used envelopes with rapid onset or termination times during this year so that the two experimental stimuli produced did not overlap substantially in frequency. More importantly, I used rapid onset and termination times so that control and experimental stimuli would have similar SPLs over shared sound frequencies.

In 1999, I produced experimental stimuli with equal onset and termination times and with overall duration times equal to half of the whole-call control stimulus's duration (52.5 ms, Fig. 1C). I used equal onset and termination envelope duration times during this year to determine if the envelopes that I used in generating 1998 experimental stimuli might explain the results that I obtained in 1998.

Preliminary playback trials conducted in 1999 indicated that 1999 half-call stimuli could not be amplified to an RMS SPL equal to, or even approaching, an 80-dB RMS level as could half-call stimuli produced in 1998. Instead, results of preliminary trials suggested that I needed to use an onset envelope that was similar to the envelope used to generate the whole-call stimulus. As a result, 1999 half-call stimuli have an overall RMS amplitude of only ~70 dB (Fig. 1).

I did not produce amplified versions of 1998 stimuli, but produced amplified (+6 dB) versions of 1999 stimuli, in part because I suspected that subjects might not approach these short duration stimuli unless they were played well above ambient noise levels. Use of a triangular envelope produced a low level of spectral smearing in digital signals near peak SPL, but this smearing was of negligible magnitude in spectra of calibrated recordings obtained at a distance of 1.0 m.

Stimulus playback

I wrote stimulus sound files to an audio format recordable compact disc (CD-R, Philips CDD 2600, 16-bit, 44.1 kHz) for playback in the field using an audio compact disc player (Sony CDX-C560 and Bescor 14 V battery). In 1998, stimuli were written to a single sound file as pairs with a 0.3-s period of silence inserted between each stimulus copy. This 0.3-s period of silence was inserted so that paired stimuli would simulate a highly "motivated" conspecific rival. This period was short enough to prevent subjects from moving more than a few cm during the 0.3-s period between stimuli. The CD player was turned off as soon as a subject appeared to respond to a playback (as described below). In 1999, only a single stimulus was written to each sound file because, while some subjects appeared to respond more strongly to stimuli when paired in 1998, others appeared to often adapt quickly to the paired stimuli and respond rarely. I controlled single and paired stimuli that were played to subjects during each trial using a remote control.

Stimuli were played from an upward oriented 3/4-inch dome speaker (Infinity reference 110T). I calibrated SPL for playback at a distance of 1.0 m over 360° in the horizontal plane using a microphone (Brüel and Kjaer 4189) placed 1.0 m from the upward oriented dome speaker (Fig. 1 inset), microphone preamplifier (Brüel and Kjaer 2671), microphone to line-level preamplifier (Radio design labs STM-2), acoustic calibrator (Brüel and Kjaer 4231) microcomputer (Apple PowerBook 3400c) and Canary 1.2 software (Charif et al. 1995). I obtained all calibration measurements 2 m above the ground in an open field with two acoustic foam panels [Cutting Wedge, 122×122×7.6 cm (48×48×3 inch), Systems Development Group] stacked on the ground beneath the speaker and the microphone. I adjusted stimulus amplitude digitally so that a single digitally scaled CD player "volume" setting produced a known reference source SPL. I then compensated for spectral variation in the speaker's output using a digital parametric equalizer (Q10, Waves, Tel-Aviv, Israel, and SoundEdit 16, Macromedia). A linear frequency sweep (~84 dB SPL, 1.5–5.5 kHz) was played and recorded repeatedly (using equipment just described) until I had removed all spectral deviations greater than ±0.5 dB between 1.8 and 5 kHz over 360° in the horizontal plane and over ±15° in the vertical plane (Fig. 1, inset). The speaker's upward orientation allowed for correction over 360° horizontal degrees. Despite the speaker's upward orientation, corrections no larger than 2 dB (1.8–5 kHz) were required within ±15 vertical degrees under these free-field conditions. RMS SPL increased slightly above 15 vertical degrees, depending on sound frequency, but playbacks were never presented to subjects positioned above this angle.

Playback protocol

Playback trials were initiated when a subject could be attracted to a perch near a territory boundary using a second speaker playing un-calibrated calls or songs not used as experimental stimuli [Polk Audio MM 3000, 2.54-cm (1-inch) dome, Sony WM-D6C tape recorder, Radio Design Labs ST-PA6 amplifier]. Once a subject perched near this first speaker (±5 m) I began playing test stimuli from the second calibrated speaker (described previously) positioned 1±0.1 m above the ground in a random direction (±10°) leading into what was determined as the center of each subject's defended territory. The distance of this second calibrated speaker from the location of each subject's starting perch was from 20 to 40 m in trials conducted with an amplified (+6 dB) stimulus and from 10 to 40 m in all other trials (mean±SD speaker distance from initial position of subject = 20.0±5.6 m, all playbacks; 18.0±4.2 m, -6-dB playbacks; 19.3±4.4 m, ±0-dB playbacks; 26.3±6.3 m, +6-dB playbacks). In all cases, the exact distance from the starting perch to the speaker playing test stimuli depended on the location of each subject's starting perch relative to the location of the second calibrated speaker. When multiple playbacks were required call stimuli were played to subjects at a rate of approximately ten calls per minute. As described above, stimuli in 1998 were played in pairs, but were played individually in 1999. Playbacks were terminated if a subject did not respond within 30 playbacks. To prevent triangulation on the sound source I terminated playback the instant a subject moved more than 1 m horizontally or vertically from his original perch.

I attempted to play all of each year's stimuli to each individual subject, on different days, over the course of a week and a half. In many cases, subjects stopped landing near their starting perches for reasons unknown to me or repeatedly flew a short distance (>~1 m) from this perch just as experimental stimuli were presented from the second playback speaker. As a result, I was unable to run all trials with each subject. To ensure an adequate sample size of trials conducted with attenuated stimuli in 1998, 11 of 25 subjects received playbacks of attenuated stimuli before being played stimuli at a normal 80-dB SPL. Apart from this exception, playbacks were presented in a random order.

I videotaped each subject's starting perch and subsequent perch locations for a period of five minutes after subjects first took flight (Cannon ES6000 in 1998 or Sony TRV-900 with 2× telepho-

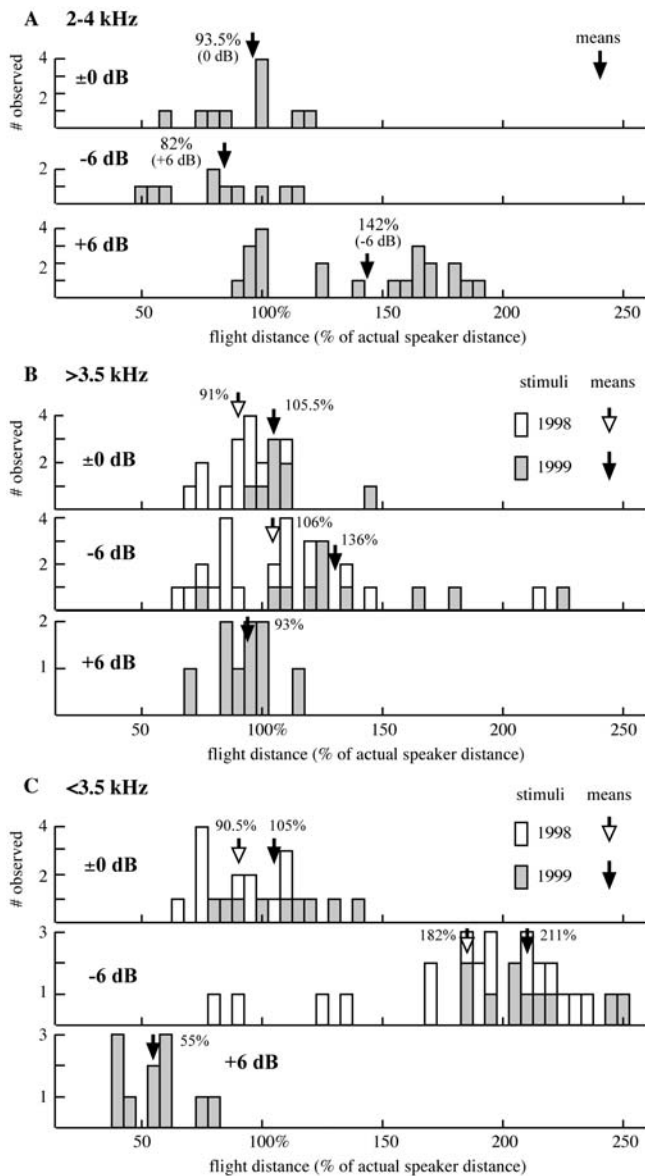


Fig. 2A–C Farthest distances flown as a percentage of actual speaker distance. *Arrows* indicate mean distances flown in response to each stimulus. Subjects judged distance accurately when played stimuli at a normal 80-dB SPL (**A**), (± 0 dB) and when played half-call experimental stimuli produced with sound frequencies above ~ 3.5 kHz (**B**). In contrast, subjects often misjudged speaker distance when played attenuated (-6 dB) or amplified ($+6$ dB) whole-call control stimuli (**A**) and nearly always misjudged speaker distance when played attenuated or amplified half-call experimental stimuli produced with sound frequencies below ~ 3.5 kHz (**C**). These results suggest that subjects use SPL as an auditory distance cue when they approach playbacks of SPL altered stimuli produced with sound frequencies below ~ 3.5 kHz but use another cue when they approach stimuli produced with sound frequencies above ~ 3.5 kHz

to lens in 1999). Subjects usually flew low but above dense vegetation to a conspicuous perch. As a result, I was able to videotape and subsequently locate accurately nearly all perch locations immediately after each trial with minimum potential for observer error. I recorded all perch locations but chose as a single measure of flight distance the perch farthest from the starting perch (see Nelson and Stoddard 1998).

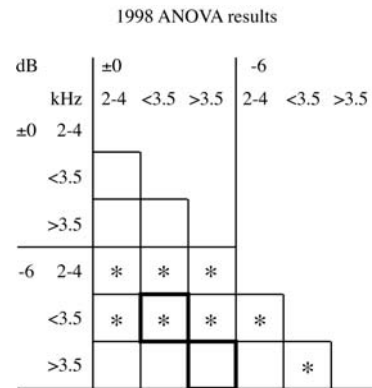


Fig. 3 Significant differences (*) observed in 1998 playback trials (modified LSD, $P < 0.05$). Differences delineated with thickened lines are contrasts between half-call stimuli played at 80 dB and the same stimuli played with altered SPL (-6 dB). These differences are identical to results obtained when both 1998 and 1999 results are pooled

Results

Subjects took flight after being played an average of 5.6 ± 6 stimuli (mean \pm SD; subjects flew after two playbacks in 39% of trials, after four in 24% of trials and after six in 13% of trials) and there was no significant difference in the number of stimuli played before subjects flew towards playbacks of each stimulus type (ANOVA, $F_{14,164} = 0.59$, two-tailed, $P = 0.87$). While not significantly different, I had to play a greater number of attenuated half-call stimuli produced in 1999 in comparison with other stimuli, presumably because these stimuli have a relatively low overall RMS SPL (~ 70 dB), low peak SPL and short duration (Fig. 1). In addition, a greater number of subjects in 1999 did not respond to attenuated half-call stimuli after the maximum number of 30 playbacks and these trials had to be attempted on another day. As in previous investigations (Nelson and Stoddard 1998; Nelson 2000), neither the number of calls played before flight nor the order in which the stimuli were played influenced how accurately towhees assessed distance to the speaker. Subjects stayed in a horizontal plane about 1.5 ± 1 -m deep throughout the experiment (mean \pm SD elevation of starting perches = 1.9 ± 0.85 m and landing perches = 1.55 ± 0.7).

Subjects approached attenuated (-6 dB) and amplified ($+6$ dB) whole-call stimuli as predicted and observed in previous investigations (Nelson and Stoddard 1998; Nelson 2000). That is, subjects: (1) flew distances that were comparable to speaker distances when played the control whole-call stimulus at a normal 80 dB SPL, (2) often flew beyond actual speaker locations when played the attenuated (-6 dB) whole-call stimulus, and (3) often flew short of speaker locations when played the amplified ($+6$ dB) whole-call stimulus (Figs. 2A, 3, 4, Table 1).

Subjects accurately located all half-call stimuli that were played with a normal 80 dB SPL (Figs. 2B, C,

Table 1 Mean±SD of flight distances in response to playbacks of call stimuli

Year	Stimulus	Attenuation (dB)	Absolute SPL (dB)	Fight/speaker distance (mean±SD)	<i>n</i>
1998 and 1999	Whole	0	80	0.93±0.48	10
1998	<3.5 kHz	0	80	0.90±0.49	10
1998	>3.5 kHz	0	80	0.90±0.95	11
1999	<3.5 kHz	0	80	1.04±0.86	10
1999	>3.5 kHz	0	80	1.05±0.52	9
1998 and 1999	Whole	-6	74	1.42±0.43	23
1998	<3.5 kHz	-6	74	1.81±0.59	18
1998	>3.5 kHz	-6	74	1.05±0.75	19
1999	<3.5 kHz	-6	74	2.11±0.04	10
1999	>3.5 kHz	-6	74	1.36±0.26	10
1999	whole	+6	86	0.82±0.34	10
1999	<3.5 kHz	+6	86	0.55±0.38	11
1999	>3.5 kHz	+6	86	0.93±0.05	9
1998 and 1999	<3.5 kHz	0	80	0.97±0.68	20
1998 and 1999	>3.5 kHz	0	80	0.97±0.50	20
1998 and 1999	<3.5 kHz	-6	74	1.92±0.11	28
98 and 99	>3.5 kHz	-6	74	1.16±0.28	29

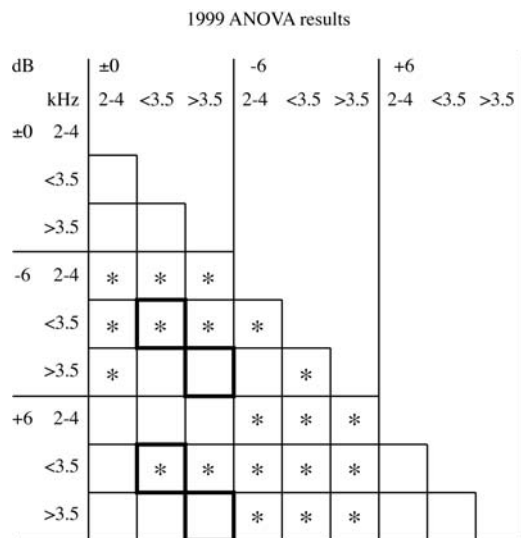
**Fig. 4** Significant differences (*) observed in 1999 playback trials (modified LSD, $P<0.05$). Differences delineated with thickened lines are contrasts between half-call stimuli played at 80 dB and the same stimuli played with altered SPL (-6 dB and +6 dB)

Table 1). In addition, subjects accurately located half-call stimuli that were produced with sound frequencies above 3.5 kHz despite variation in source SPL (Figs. 2B, Table 1). In contrast with these results, subjects flew either longer or shorter distances in response to attenuated (-6 dB) or amplified (+6 dB) half-call stimuli that were produced with sound frequencies below 3.5 kHz in both 1998 and 1999 (Figs. 2C, Table 1).

I played six stimuli to subjects in 1998 and nine stimuli to subjects in 1999. As a result, numerous statistical comparisons can be drawn (Figs. 2, 3, 4). Most importantly, subjects flew significantly farther distances in response to the low frequency (<3.5 kHz) half-call stimulus played in 1998 with attenuated SPL (-6 dB) in comparison with distances flown in response to the same

stimulus played at 80 dB (± 0 dB; ANOVA, $F_{5,85}=18.21$, $P<0.0001$, modified LSD (Bonferroni), $P<0.05$, Fig. 3). Subjects also flew significantly farther or shorter distances in response to the low frequency (<3.5 kHz) half-call stimulus played in 1999 with attenuated or amplified SPL (-6 dB or +6 dB) in comparison with distances flown in response to the same stimulus played at 80 dB (± 0 dB; ANOVA results, $F_{8,93}=27.39$, $P<0.0001$, modified LSD (Bonferroni), $P<0.05$, Fig. 4). Finally, subjects flew significantly farther distances in response to attenuated (-6 dB) half-call stimuli produced with low frequencies (<3.5 kHz) when flights from these 2 years were pooled (ANOVA, $F_{5,124}=30.40$ $P<0.0001$, modified LSD (Bonferroni), $P<0.05$, Fig. 3).

Discussion

Relationship between sound propagation and auditory distance perception

Towhees misjudged distance to attenuated and amplified (-6 or +6 dB) half-call experimental stimuli when these stimuli were produced with sound frequencies below 3.5 kHz, but did not misjudge distance when stimuli were produced with sound frequencies above 3.5 kHz. These results suggest that towhees use SPL as an auditory distance cue when they hear sound frequencies below ~3.5 kHz, but use a second, as of yet unidentified, cue when they hear sound frequencies above ~3.5 kHz.

How sound propagates, on average, through Florida scrub habitat has likely influenced how towhees assess auditory distance. Sound frequencies below ~3.5 kHz tend to propagate with less attenuation over distance and tend to propagate with more reliable attenuation in comparison with higher sound frequencies (Nelson, submitted). That is, sound frequencies below ~3.5 kHz propagate with less variation in attenuation across sites sampled, across several speaker and microphone elevations

and between days. As a result, it is not surprising that towhees use SPL as an auditory distance cue when they assess distance to stimuli produced with sound frequencies below ~ 3.5 kHz.

Influence of experimental amplitude envelopes

Despite the abnormal amplitude envelopes and short duration times of half-call experimental stimuli (Fig. 1B, C), subjects often approached these stimuli nearly as directly and as vigorously as they approached whole-call control stimuli (Fig. 1A; see also Nelson and Stoddard 1998; Nelson 2000). Thus, subjects presumably perceived all of these stimuli as being produced by a rival conspecific.

Subjects did not assess actual or virtual speaker distance as accurately as in previous studies when played whole-call stimuli (Nelson and Stoddard 1998; Nelson 2000). However, this increase in error may be due to the abnormal amplitude envelope applied to the whole-call control stimulus in this experiment (with maximum SPL occurring at 50% of overall call duration as opposed to a more typical location near 65%, Fig. 1). That is, subjects might be expected to fly a distance shorter than predicted because they appear to pay greatest attention to sound frequencies below ~ 3.5 kHz when they use SPL as an auditory distance cue and because the amplitude envelope applied to this stimulus functioned to increase SPL near and below ~ 3.5 kHz and decrease SPL above ~ 3.5 kHz (relative to the normally observed SPLs over these same respective sound frequency ranges).

Subjects continued to rely on SPL when played the low frequency half-call experimental stimulus produced in 1999 despite the fact that this stimulus was produced with an onset amplitude envelope that approximated only the initial 52.5 ms of the 105-ms whole-call control stimulus's onset envelope. In addition, this 1999 stimulus had a low overall RMS and peak SPL in comparison with the control stimulus and with 1998 half-call experimental stimuli. Nonetheless, responses to both 1998 and 1999 low frequency half-call experimental stimuli are similar and towhees nearly always appeared to use SPL when played either stimulus. These results suggest that towhees may often be able to estimate both source SPL and amount of attenuation after listening to only the initial 52.5 ms of a natural 210 ms, 80 dB call.

Is SPL a reliable or deceptive cue?

Towhees commonly misjudge speaker distance when played SPL altered call stimuli produced with sound frequencies below ~ 3.5 kHz. However, there is no evidence to suggest that towhees normally vary source SPL unpredictably when calling and, as a result, there is no reason to assume that SPL does not usually function as a reliable auditory distance cue. Nonetheless, the potential for manipulation exists. For example, if towhees are able to

occasionally vary source SPL without varying correlated spectral and temporal variables then towhees may occasionally be able to appear farther away or closer to a listener than they actually are. In all cases, however, the potential for deceptive manipulation of SPL may need to be viewed in a broader context. For example, if correlations with SPL develop from physical forces involved in vocal production (e.g., if SPL and correlated variables vary with sub-syringeal air pressure, Suthers and Goller 1997), then variation is likely to convey additional information that may only be indirectly associated with sound source location (Nelson 2000; Eriksson and Traunmuller 2002).

Duplex sound localization

The duplex theory of directional hearing suggests that interaural time difference (ITD) functions as the dominant cue to azimuth over relatively low sound frequencies, while interaural intensity difference (IID) functions as the dominant cue to azimuth over relatively high sound frequencies (Rayleigh 1907; Stevens and Newman 1936; Moushegian and Jeffress 1959). Humans, for example, appear to rely predominantly on ITD when localizing sound frequencies below ~ 1.5 kHz but appear to use IID (or spectral cues) when localizing sound frequencies above ~ 1.5 kHz. In addition, both birds and mammals appear to process ITD and IID within separate anatomical pathways (e.g., Caird and Klinke 1983; Takahashi et al. 1984; Heffner and Masterton 1990; Irvine 1992).

Towhees appear to use SPL as an auditory distance cue when they hear sound frequencies below ~ 3.5 kHz but appear to use a second auditory distance cue when they hear sound frequencies above ~ 3.5 kHz. As a result, I suggest that auditory distance perception in the towhee might also be described as being duplex.

Cue segregation in a duplex system

Accurate estimates of both source SPL and incident SPL are required if SPL is to function as a reliable auditory distance cue. However, both IID and spectral cues to azimuth are likely to interfere with absolute judgments of incident SPL simply because, by definition, these cues function well only when there is variation in incident SPL as a function of sound frequency and direction of sound incidence (Fig. 5; Blauert 1997). Furthermore, it is well known that variation in IID often results in variation in ITD (e.g., Gleich and Narins 1988; Klump 2000) and, while augmentation of ITD that is due to this interaction might be viewed as beneficial, variation might also be viewed as a source of interference. I suggest that cues to both distance and direction may often function best over separate sound frequency ranges so that interference between cues can be minimized over midrange sound frequencies where vocalizations often have substantial

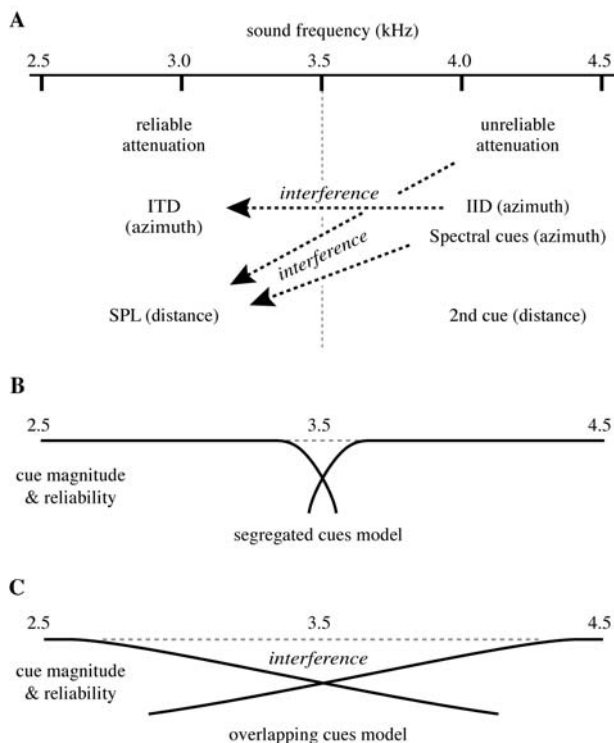


Fig. 5 **A** Schematic summary of interference likely to occur between cues to both distance and azimuth. IID and spectral cues are likely to interfere with the use of SPL as an auditory distance cue because, by definition, these cues function well only when there is adequate variation in incident-SPL. Additional sources of interference are described in the text. **B** Cue interference can be avoided over midrange sound frequencies if cues coexist and function only over a relatively narrow range of common sound frequencies (segregated cues model). **C** Alternatively, interference may compromise sound localization over a relatively broad range of sound frequencies if cues coexist and function over overlapping sound frequency ranges (overlapping cues model)

energy (Fig. 5B). I propose this model as an alternative to a more conventional model in which different sound localization cues might interfere with one another over overlapping sound frequency ranges (Fig. 5C). These alternative models are important to consider in this study because all of the stimuli I played to subjects have substantial energy at or near 3.5 kHz, yet subjects chose to use only a single cue when played half-call stimuli spanning sound frequencies to each side of this midrange sound frequency (Fig. 1).

ITD is thought to function as an important cue to azimuth in small birds (Klump and Larsen 1992). However, because small birds may often be unable to phase lock to sound frequencies above ~ 3 kHz (Gleich and Narins 1988), IID is likely to function as a second cue to azimuth over relatively high sound frequencies (Klump 2000). These lines of evidence are consistent with the use of a duplex sound localization strategy. In fact, an under-representation of inferior colliculus neurons sensitive to mid-range sound frequencies has been observed in several avian species (e.g., Calford et al. 1985; Calford 1988) and is predicted to occur between ~ 2.5

and 3.5 kHz in a small bird like the eastern towhee (Calford 1988; although see Lewald 1990).

Alternative explanations and interpretations

One potential alternative explanation for the flight distances observed in response to half-call stimuli may be that towhees normally learn to use a judgment of lowest frequency, or related judgment, to estimate source SPL (Nelson 2000). If so, subjects may have been unable or unprepared to estimate source SPL when played half-call stimuli with sound frequencies above ~ 3.5 kHz. In fact, source SPL is strongly correlated with lowest frequency and lowest frequency measurements rarely exceed 3 kHz (Nelson 2000).

A second alternative explanation may be that towhees did not use SPL as an auditory distance cue when played half-call stimuli produced with sound frequencies above ~ 3.5 kHz because these stimuli span a relatively narrow range of sound frequencies (~ 0.5 kHz). In fact, other species tend to assess azimuth most accurately when played stimuli that span a relatively broad range of sound frequencies (e.g., Knudsen and Konishi 1979). Thus, while towhees did not assess distance less (or more) accurately when played half-call stimuli at a normal source SPL (80 dB), it can be argued that bandwidth might have influenced whether subjects were able to use SPL as an auditory distance cue. On the other hand, there is no clear reason to assume that a stimulus spanning ~ 0.5 kHz (i.e., $\sim 1/5$ th octave; ~ 1 kHz with side-bands) should be described as having a narrow bandwidth. More importantly, this interpretation does not explain why subjects nearly always used SPL when played low frequency half-call stimuli. Furthermore, while subjects appeared to use SPL when played both whole-call (~ 2.5 – 4 kHz) and low frequency half-call stimuli (~ 2.5 – 3.5 kHz), subjects were most likely to use SPL when played the half-call stimulus with the narrower bandwidth (~ 1 vs 1.5 kHz). A duplex sound localization strategy provides a consistent explanation for these results and suggests that an increase in stimulus bandwidth may have the greatest influence when the increase results in the inclusion of sound frequencies both above and below ~ 3.5 kHz.

Implications for the use of frequency dependent attenuation

Low frequency half-call stimuli played in this study are not markedly different from stimuli that have undergone substantial frequency dependent attenuation. In fact, other investigators have used low-pass filters below 3.5 kHz to emulate a level of frequency dependent attenuation that is natural in other habitats (e.g., 3 kHz, Naguib 1995, 1997). Subjects in this study judged auditory distance accurately when played low frequency (< 3.5 kHz) half-call stimuli at a normal 80-dB SPL and these results

suggest that towhees do not use frequency dependent attenuation as an auditory distance cue.

Previous investigators commonly infer that subjects use frequency dependent attenuation when subjects respond differently, or move farther, in response to playbacks of low-pass filtered stimuli (e.g., Naguib 1995; Naguib and Wiley 2001). However, this study may provide an alternative explanation for these results. For example, subjects also may have used overall (absolute) SPL as a cue to distance if unfiltered sound frequencies attenuate reliably over distance in comparison with filtered frequencies. Furthermore, subjects may have responded differently, or moved farther, if they were predisposed to use SPL by the elimination of sound frequencies above ~3–4 kHz. Unfortunately, these two hypotheses are difficult to resolve because stimuli in these previous experiments have been played to subjects only at a single consistent source SPL and this SPL may have been either higher or lower than the natural level that subjects expected for each stimulus.

There also may be little reason to assume that frequency dependent attenuation correlates more reliably with auditory distance than overall (absolute) attenuation over relatively low sound frequencies. In fact, substantial variation in attenuation over relatively high sound frequencies is expected to occur in all habitats and is likely to interfere both with reliability of frequency dependent attenuation and overall attenuation. I suggest that towhees use neither overall attenuation above 3.5 kHz nor frequency dependent attenuation as cues to distance because sound frequencies above ~3.5 kHz neither attenuate reliably on an absolute scale nor in relation to lower sound frequencies.

Generality of results and interpretations

Vocalizations produced by birds throughout North America span a range of sound frequencies between about 1 and 12 kHz; however, most vocalizations span a range of sound frequencies between 2 and 5 kHz (Wiley and Richards 1982). Thus, towhee calls in Florida do not span an unusual range of sound frequencies (2–5 kHz).

I describe a duplex sound localization strategy in this study. However, songbirds are already known to employ duplex vocal production strategies and, in fact, one such strategy is the independent (i.e., lateralized) production of sound frequencies to each side of ~3.5 kHz (e.g., Suthers 1997, 1999). Vocal production mechanisms in birds have presumably coevolved with auditory mechanisms and, as a result, duplex communication strategies may often help to define important sound frequency ranges in bird vocalizations. For example, canaries, *Serinus canaria*, often produce two-note syllables that span sound frequencies to each side of ~3.5 kHz and these syllables are known to elicit high levels of sexual display in females (Vallet et al. 1998).

Reliability of sound attenuation over distance has been quantified as a function of sound frequency only in

Florida scrub habitat and, as a result, it remains difficult to predict which avian species might use similar cues. On the other hand, it seems unlikely on a priori grounds that the eastern towhee in Florida has evolved a unique auditory system for judging distance. Thus whether other species might employ a duplex auditory distance assessment strategy will remain unclear until several requisite factors, such as the ability to estimate source SPL, have been investigated in other species.

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