



# Avian dependence on sound pressure level as an auditory distance cue

BRIAN S. NELSON

Department of Biological Sciences, Florida International University

(Received 19 November 1998; initial acceptance 12 February 1999;  
final acceptance 8 September 1999; MS. number: A8196R)

Sound pressure level (SPL) has received little attention as a distance cue or signal for communication because of the methodological difficulty of determining source SPL from free-ranging signallers and because SPL is presumed to be unreliable as a distance cue. Eastern towhees, *Pipilo erythrophthalmus* (Emberizidae, Passeriformes), in south-central Florida give a simple call during territorial interactions. I obtained measurements of call-source SPL with a calibrated microphone positioned  $100 \pm 10$  cm from caged male eastern towhees. Measurements of source SPL were highly variable, but much of this variation can be predicted from measurements of call duration or call frequency variables (spectrotemporal variables). Male towhees accurately perceived the distance of a speaker after it played synthetic calls that matched the amplitude and structure of natural 84-dB and 78-dB call types. Subjects flew further in response to an attenuated ( $-6$  or  $-12$  dB) version of an otherwise identical 84-dB call and flew shorter in response to an amplified ( $+6$  dB) version of this same call. Towhees misjudged speaker distance in approximately half of the trials that included a discrepancy ( $-6$ ,  $-12$  or  $+6$  dB SPL) between playback source SPL and predicted spectrotemporal variables. These distance errors suggest that towhees assess auditory distance partly from the difference between perceived SPL and source SPL, determined from spectrotemporal variables.

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Accurate auditory distance perception can play a critical role in moderating physical social interaction. Unnecessary or dangerous interactions can be avoided using a spacing mechanism (Whitney & Krebs 1975; Awbrey 1978; Wilczynski & Brenowitz 1988), or can be avoided across a stable territory boundary if a defender can track or survey locations of rival conspecifics.

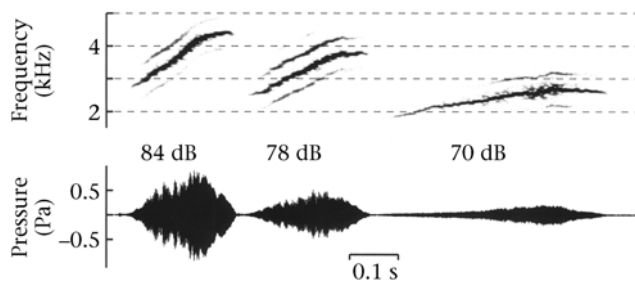
Sound is subject to 'degradation' during propagation as a result of frequency-dependent attenuation and the addition of scattered and refracted sound with direct sound (Morton 1982; Wiley & Richards 1982). Degradation has received the greatest attention as an auditory distance cue for free-ranging birds (e.g. Richards 1981; Morton 1982; McGregor 1994; Naguib 1998). Studies demonstrate that an increase in song degradation produces behaviour consistent with the perception of increased auditory distance. None the less, it remains unclear whether degradation is a reliable distance cue in all habitats (Dabelsteen et al. 1993; Mathevon et al. 1996; Nelson & Stoddard 1998).

Sound pressure level (SPL) decreases approximately 6 dB per doubling of distance from a point sound source

\*Correspondence: B. S. Nelson, Department of Biology, Indiana University, Jordan Hall 142, Bloomington, IN 47405, U.S.A. (email: [bnelson@bio.indiana.edu](mailto:bnelson@bio.indiana.edu)).

in the free field. Attenuation of SPL is a salient distance cue for humans in open, nonreverberant environments (Mershon & King 1975; Nielsen 1993) and frogs are known to use SPL as an intermale spacing mechanism (Brenowitz 1989). Birds can detect small changes in incident SPL (Dooling 1982) and can regulate or control SPL during production (Cynx et al. 1998; Manabe et al. 1998). None the less, SPL is thought to be an unreliable distance cue when excess attenuation is unpredictable (Morton 1982; Wiley & Richards 1982), or when signallers vary source SPL unpredictably over time (Morton 1982). Thus, Naguib (1997) used changes in relative SPL within playback trials (meant to simulate an approaching or retreating territorial rival), as opposed to absolute changes in SPL between trials, to investigate use of SPL as an auditory distance cue and found behaviour consistent with the perception of increased distance when a retreat was simulated (i.e. when SPL was decreased by 6 dB).

During territorial interactions with conspecifics, both male and female eastern towhees, *Pipilo erythrophthalmus* (Emberizidae, Passeriformes), give a call that is highly variable in frequency, duration and source SPL (Fig. 1). This vocalization is not produced by eastern towhees isolated as nestlings from wild populations, suggesting that use of this call might be a learned behaviour (Ewert



**Figure 1.** Time spectrograms and waveforms of calls given by three individuals demonstrating gradation in spectrotemporal variables and sound pressure level (RMS SPL re 20  $\mu$ Pa, noted above each waveform).

1979; Greenlaw 1996). Towhees give this call as an alarm, when mobbing predators, and when calling to mates over both long and short distances within a territory.

I recorded calls from caged male eastern towhees in south central Florida. Source SPL is variable, and I demonstrate with regression that much of this variation can be explained by call duration or any of several measured call frequency variables that vary closely with source SPL, including the lowest and highest call frequency, the frequency of a call at peak SPL, the range of frequencies spanned and the call duration. I will henceforth refer collectively to call duration and these several call frequency variables as spectrotemporal variables. SPL and dominant frequency are also positively correlated in calls produced by the cricket frog, *Acris crepitans*, and this correlation is thought to occur either as a result of variation in radiation efficiency, or as a result of variation in pulmonary air pressure (William E. Wagner, Jr, personal communication). Measurements of SPL are also positively correlated with subsyringeal air sac pressure in song syllables produced by the northern cardinal, *Cardinalis cardinalis* (Suthers & Goller 1997). Both of these results suggest that correlations between source SPL and spectrotemporal variables may be passive elements of these sound production mechanisms.

Spectrotemporal variables are subject to minimum alteration during propagation and I predicted that listeners use call spectrotemporal variables to estimate call-source SPL. If towhees use call spectrotemporal variables to predict source SPL, and use SPL as an auditory distance cue, subjects should fly to speaker locations (with minimum error) when calls are played at an appropriate SPL (predicted using regression equations described). However, subjects should underestimate the distances of speaker locations in response to calls played at a greater than predicted SPL and should overestimate the distance of speaker locations in response to calls played at a lower than predicted SPL.

I present data from a field experiment suggesting that eastern towhees use SPL attenuation as an auditory distance cue. These data further indicate that perception of auditory distance is dependent on an accurate estimation of source SPL derived from at least one spectrotemporal variable. Use of SPL as an auditory distance cue, despite substantial variation in source SPL, demonstrates that the

towhee recognizes and pays attention to at least one described relationship between spectrotemporal variables and SPL.

## EXPERIMENT 1: SPECTROTEMPORAL ASSOCIATION WITH SPL

### Methods

I recorded towhee calls (e.g. Fig. 1) given by 19 male eastern towhees defending territories within a 10-km<sup>2</sup> area at Archbold Biological Station, 12 km south of Lake Placid, Florida from May to July 1995. To maintain a consistent recording distance, I captured subjects in a mist net and placed them in a vinyl-coated steel wire cage measuring 20 × 20 × 20 cm (with mesh size 1.15 × 2.25 cm and 2.4-mm diameter wire) and elevated 150 ± 20 cm above the ground in a small clearing or fire-lane at a location within each bird's defended territory. I placed a microphone (Brüel & Kjaer 4188) perpendicular to the ground, 100 cm from the centre of the cage, and recorded calls from the AC output of a sound level meter (Brüel & Kjaer 2236) using a digital audio tape recorder (Sony TCD-D3). Birds were free to move in this cage and thus the actual recording distance was 100 ± 10 cm. I recorded a 94-dB 1-kHz reference calibration tone of an acoustic calibrator (Brüel & Kjaer 4231) immediately before and after all recordings were made so that call SPL could be determined from the recordings. If subjects did not begin to call on their own within a few minutes of being placed in the cage, I elicited calls by playing conspecific vocalizations of variable-source SPL from a distant location. I could not quantify how playbacks influenced recorded calls because I did not control the source SPL of these playbacks and did not standardize speaker locations relative to neighbours or territory boundaries. After recording I colour-banded subjects for later identification.

### Call analysis

Recordings were digitized on a computer (Macintosh 660AV, 16-bit A/D, 48.1-kHz sampling rate). I measured spectrotemporal variables directly from time spectrograms produced with Canary 1.2 software (Charif et al. 1995). Spectrotemporal variables measured from time spectrograms included the highest and lowest frequency, the frequency at peak SPL (a Canary time-spectrogram measurement variable; Charif et al. 1995), the range of frequencies spanned, and the call duration. Spectrotemporal measurements were standardized by scaling calls digitally relative to a single reference SPL calibration tone and by measuring variables from time spectrograms displayed with single brightness (82%) and contrast (100%) settings. I ignored side bands and measured peak SPL and root mean square (RMS) SPL directly from calibrated call waveforms selected when measuring call duration from time spectrograms. Unless otherwise noted, all decibel measurements are given as RMS SPL re 20  $\mu$ Pa.

### Sample selection and statistical analysis

I recorded 5–39 calls (mean 17.4) from 19 subjects in 1995 and selected for analysis five calls at random from recordings of each subject. I used both simple and multiple logarithmic regression (Norušis 1994) to investigate associations with spectrottemporal variables that might allow towhees to estimate source SPL. I used regression, as opposed to correlation, to obtain regression equations and measurements of standard error.

I conducted regression analyses using both individual calls and average values from each bird as my unit of analysis. While these analyses are not independent statistically, both are relevant biologically and necessary for a meaningful analysis of methodological error. Towhees often respond to the playback of only a single call (personal observations). However, in nature they may often have an opportunity to listen to several conspecific calls before responding, suggesting that an analysis of mean values is also relevant biologically. Similarly, an analysis of mean values can approximate more closely the variation that towhees are likely to encounter in nature when estimating source SPL (see Discussion).

### Signaller orientation

I measured the amount of variation in SPL measurements due to variation in signaller orientation by recording 220 calls from five additional males in June 1997 (33, 42, 47, 48 and 50 calls recorded from each bird, respectively). Before recording these five birds, I placed two acoustic foam panels (cutting wedge 48 × 48 × 3 inches, 122 × 122 × 7.6 cm, Systems Development Group, Frederick, Maryland) on the ground between the cage and microphone to absorb reflection from the ground. I videotaped the birds (Sony CCD-V8 AF) from a position slightly above and behind the microphone (Brüel & Kjaer 4189) during audio recording to determine each bird's orientation and position in the cage at a later time. Recordings were digitized in the field using an Apple PowerBook 1400c, microphone to line-level preamplifier (Radio Design Labs STM-2), microphone preamplifier (Brüel & Kjaer 2671) and 0.5-inch (1.27-cm) free-field microphone (Brüel & Kjaer 4189). Otherwise I recorded calls and obtained measurements of SPL and spectrottemporal variables as described above for experiments conducted in 1995.

## Results

The SPL of 95 randomly selected calls recorded 100 cm from caged subjects ranged from 74 to 88 dB (Fig. 2). Call duration was associated inversely with call-source SPL and all measured frequency variables were associated positively with call SPL (Tables 1, 2, Fig. 2,  $P < 0.002$ , all cases). Root mean square (RMS) SPL, measured over each call's calibrated waveform, was strongly associated with peak SPL ( $r^2 = 0.95$ ,  $SE = 0.78$ ,  $P < 0.0001$ ). As a consequence, the strength of the associations between source SPL and spectrottemporal variables changed little when measurements of peak SPL were substituted for measurements of

RMS SPL. Associations were only slightly stronger when both the lowest frequency and the frequency at peak SPL were entered as independent variables in a multiple regression model ( $r^2 = 0.73$ ,  $SE = 1.85$  among individual calls,  $r^2 = 0.86$ ,  $SE = 1.22$  among mean values).

### Signaller orientation

Orientation of the signaller's head and body had a measurable influence on SPL at a single microphone position and direction (Fig. 3). Measurements of source SPL were, on average, 2–3 dB lower when a bird's head was oriented 150–180° away from the microphone than when oriented within 30° of the microphone. Measurements were less predictable and orientation was more difficult to determine using the video recordings when a subject was oriented 30–150° away from the microphone. Changes in body orientation also produced variation in SPL at the microphone, but variation was difficult to characterize independently of variation in head orientation. Measurements of source SPL made in 1997 were, on average, 2–3 dB lower than recordings obtained in 1995. Experimental recordings of frequency sweeps and measurements of source SPL demonstrate that this decrease in measured source SPL between years can be attributed to placement of sound absorbing acoustic foam on the ground between the bird and microphone.

## EXPERIMENT 2: SPL AS AN AUDITORY DISTANCE CUE

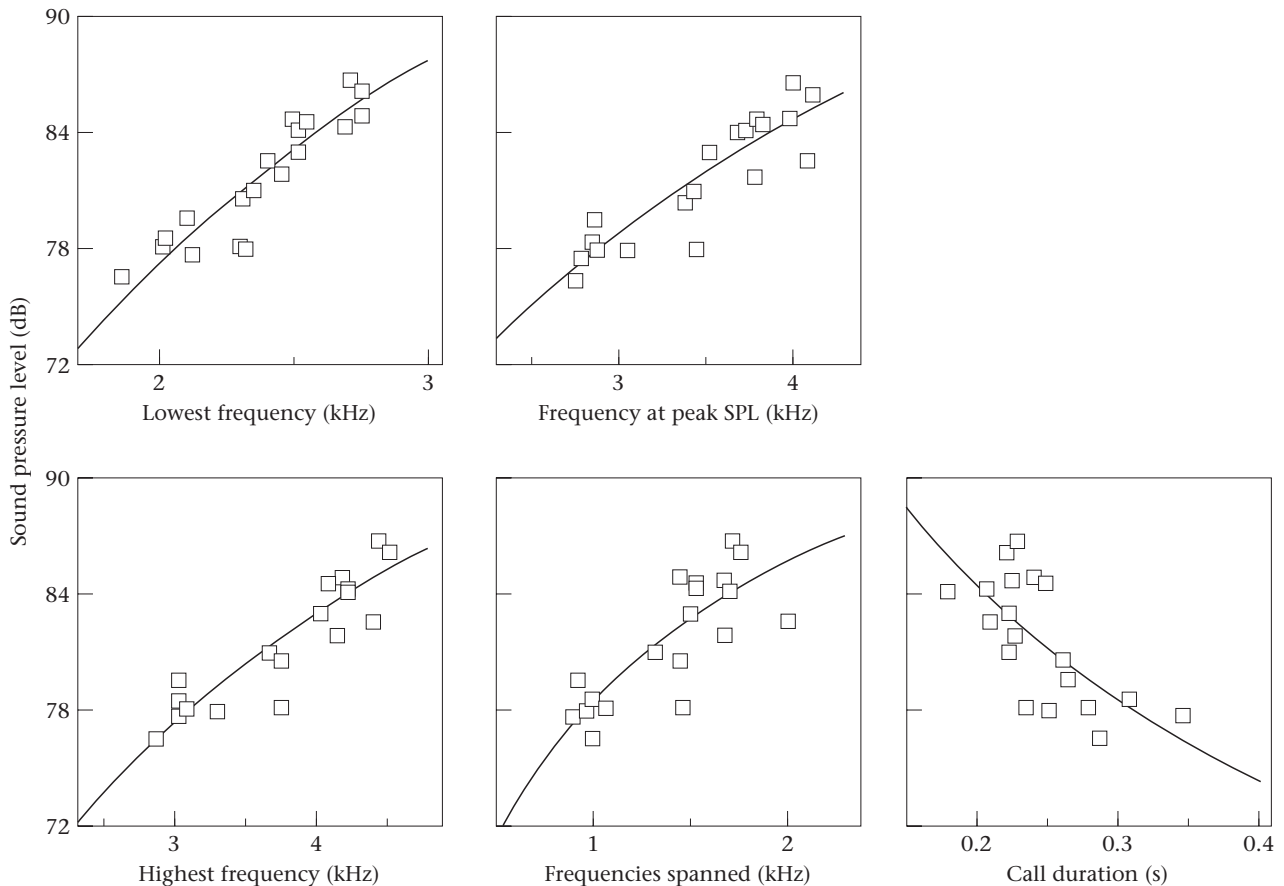
### Methods

I selected 15 male towhees as subjects, all of which frequented a conspicuous perch near their territory boundary that could be used as a starting perch during the playback trials. All 15 birds defended territories in a scrubby flatwoods vegetation community (Abrahamson et al. 1984) that had been burned within the previous 5 years.

If towhees use spectrottemporal variables to predict source SPL, and use SPL as an auditory distance cue, I hypothesized that: (1) subjects should fly to a speaker having played a call stimulus at a source SPL predicted using described regression equations (with minimum error); (2) subjects should fly short of the speaker locations in response to calls played at a greater than predicted SPL; and (3) subjects should fly past speaker locations in response to calls played at a lower than predicted SPL.

### Playback stimuli

I tested towhee distance perception using five synthetic calls. I used synthetic calls as stimuli, as opposed to previously recorded calls, to emphasize defined spectrottemporal variables. I also chose to use synthetic stimuli to avoid subtle intracall variation that might convey additional information. I generated four stimuli for playback, with spectral and temporal values appropriate (as determined by regression analysis) for a call produced at an 84-dB source level (Fig. 4, Table 2), and a fifth



**Figure 2.** Associations between source SPL (dB re 20  $\mu$ Pa) and five measured spectrotemporal variables. Values ( $N=19$ ) are means calculated from five calls selected at random from recordings of 19 birds ( $N=95$ ). Associations suggest that towhees should be able to estimate source SPL using variables of call duration or call frequency that are subject to minimum alteration during propagation.

**Table 1.** Associations between SPL (dB RMS re 20  $\mu$ Pa) and spectrotemporal variables of towhee calls

	Lowest frequency	Highest frequency	Frequency at peak SPL	Frequency spanned	Call duration	Multiple regression model
Individual calls						
Adjusted $r^2$	0.70	0.69	0.66	0.54	0.38	0.73
SE	1.99	2.00	2.08	2.42	2.82	1.85
Mean values						
Adjusted $r^2$	0.81	0.80	0.78	0.62	0.44*	0.86
SE	1.38	1.45	1.49	1.97	2.40	1.22

\*Two-tailed  $P < 0.002$ , in all other cases two-tailed  $P < 0.0001$ . Multiple regression model with lowest frequency and the frequency at peak SPL entered as independent variables.

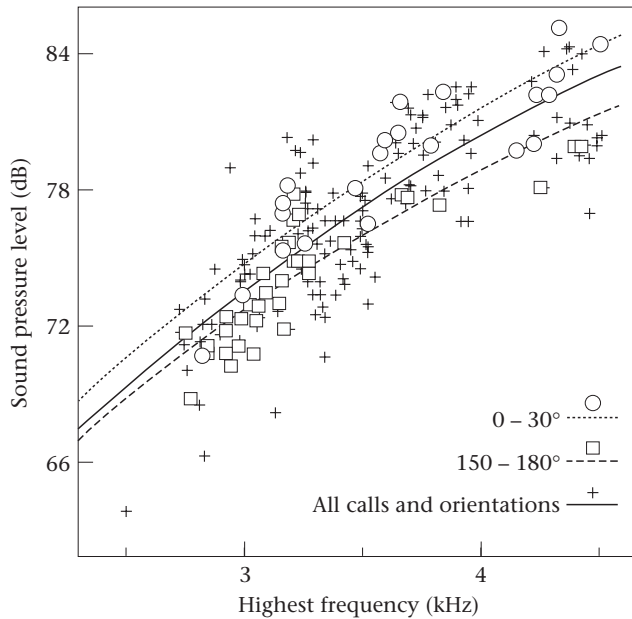
stimulus, with spectral and temporal values appropriate (as determined by regression analysis) for a call produced at a 78-dB source level (Fig. 4, Table 2). Frequency modulation (FM) was produced using a sine function and side-bands were produced in each stimulus by digitally summing attenuated ( $-20$  dB) FM signals with fundamentals 500 Hz lower and higher than the original FM signal, producing 20%, 500 Hz amplitude modulation (AM). I applied a triangular envelope to each call stimulus with peak SPL at 66% of call duration. By digitally scaling

stimulus amplitude, I broadcast 84-dB call stimuli to subjects at four different absolute SPL levels, 72, 78, 84, and 90 dB (i.e.  $-12$ ,  $-6$ ,  $-0$  and  $+6$  dB) relative to the 'natural' 84-dB level; henceforth these four stimuli are referred to as 84( $-12$ ), 84( $-6$ ), 84( $-0$ ) and 84( $+6$ ), respectively. I synthesized the fifth stimulus in a similar manner with spectral and temporal values appropriate for a 78-dB call and played the stimulus at 78 dB ( $-0$  dB); hereafter, I refer to this stimulus as 78( $-0$ ). I used both the 84( $-0$ ) and the 78( $-0$ ) stimuli as control stimuli to

**Table 2.** Logarithmic regression equations predicting call SPL (dB RMS re 20  $\mu$ Pa)

Call variable	1995 (SPL=)	1997 (SPL=) with acoustic foam
Lowest frequency	$59.76\log(F)+59.09$	$58.72\log(F)+56.60$
Frequency at peak SPL	$46.46\log(F)+56.61$	$53.77\log(F)+49.37$
Highest frequency	$43.83\log(F)+56.38$	$53.33\log(F)+48.01$
Frequency spanned	$23.36\log(F)+78.43$	$23.36\log(F)+78.43$
Call duration, $T$ (s)	$-33.27\log(T)+61.05$	$-22.92\log(T)+64.43$

$F$ : Frequency (kHz).

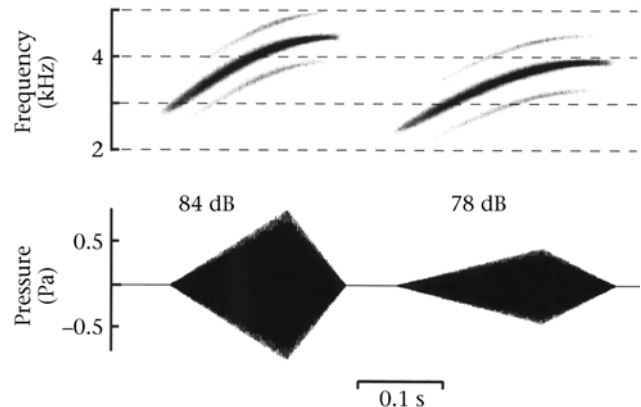


**Figure 3.** Association of source SPL (dB re 20  $\mu$ Pa) and the highest frequency demonstrating variation in measurements of SPL due to horizontal variation in head orientation ( $0^\circ$  facing the microphone). Orientation was determined from videotapes of the five birds recorded in 1997 ( $N=220$ ). Changes in both head and body orientation had a similar effect on measurements of SPL. Orientation was noted without respect to variation in posture or position in the cage.

verify that each subject was able to locate a playback speaker's location accurately when calls were played at a predicted SPL. All other stimuli were used as experimental stimuli.

#### Playback protocol

I calibrated call SPL for playback to within  $\pm 0.5$  dB using a microphone (Brüel & Kjaer 4189) placed 1.0 m from the speaker and oriented  $45^\circ$  above horizontal (Polk Audio MM 3000), a microphone preamplifier (Brüel & Kjaer 2671), a microphone to line-level preamplifier (Radio Design Labs STM-2), an acoustic calibrator (Brüel & Kjaer 4231) and a microcomputer (Apple PowerBook 1400c). I used regression equations based on calls recorded in 1995 without acoustic foam on the ground to determine spectrotemporal variables appropriate for 84-dB and 78-dB calls, and I calibrated source SPL for



**Figure 4.** Time spectrograms and waveforms of 84-dB and 78-dB variant calls synthesized for playback experiments (RMS SPL re 20  $\mu$ Pa, noted above each waveform).

playback without acoustic foam on the ground between the speaker and microphone (see Results). I played calls from a microcomputer in the field (Apple PowerBook 190cs) and amplified the calls using a line-level amplifier (Phoenix Gold PLD1 Pro line drive), power amplifier (Soundstream D200) and 1-inch (2.54-cm) dome speaker (Polk Audio MM 3000) oriented  $45^\circ$  above horizontal.

I placed one speaker (Polk Audio MM 3000) near each subject's starting perch, somewhere near a territory boundary, and attracted the subject to it by playing calls or songs not used as experimental stimuli. Once a subject perched within 1 m of the starting perch, I played a stimulus call from a second speaker positioned 15 or 25 m away in a direction leading into the subject's defended territory. The position of the second speaker was usually located near the centre of each subject's territory. Each stimulus was presented to a subject on a different day at an average rate of 20 calls/min. Silent intervals between stimuli were created by buffering stimuli with 2 s of silence and by randomly mixing buffered stimuli with 0.5- and 1.0-s silent intervals. To prevent triangulation to the sound source, or 'in-flight correction' used by barn owls (Konishi 1973), I terminated playback the instant a subject moved more than 1 m horizontally or vertically from his original perch during stimulus playback.

Each subject received one of the five stimulus types each day in a random order over the course of a single week in May 1997. I attempted to play all five stimuli to each subject. In several cases, subjects stopped landing

on their starting perches or repeatedly flew a short distance from this perch just as experimental stimuli were presented from the second playback speaker, and so was not able to conduct all trials with each bird. Three subjects continued to show a strong reaction to playback after all other trials were completed so I played an additional 84(-6) stimulus at a distance of 15 m to these three subjects and included these trials in my analysis. Flights shorter than 10 m could not be easily distinguished from movement near the starting perch. Thus, I played the 84(+6) stimulus only from a distance of 25 m so that subjects could be expected fly at least 10 m when using SPL as an auditory distance cue (see Results). Similarly, I played the 84(-12) stimulus only from a distance of 15 m so that subjects would not be expected to fly to a location near or beyond a defended territory boundary. I played all other stimuli from a distance of 15 m and occasionally from a distance of 25 m to verify that response was not dependent on speaker distance (within 25 m).

During each trial, I observed each subject's flights and noted perch locations by recording the distance and direction from a natural marker such as a coloured branch or leaf. Subjects usually flew low but above dense vegetation to a conspicuous perch. As a result, most perch locations were noted following flight with little opportunity for observer bias. I noted perch locations for a period of 5 min after subjects took flight. I transcribed and measured these locations immediately after each trial as described by Nelson & Stoddard (1998). Although I recorded all perch locations, I chose the perch furthest from the starting perch as a single measure of flight distance.

## Results

Birds took flight after 1–20 playback calls, but neither the number of calls played before flight nor the order in which stimuli were played to each subject were correlated statistically with flight distance. Throughout the experiment, the birds stayed within a mean  $\pm$  SD height of  $1.5 \pm 1$  m. Mean  $\pm$  SD height of starting perches was  $1.7 \pm 0.6$  m and landing perches were similar.

Subjects approached the speaker in response to 84(-0) and 78(-0) control stimuli with a gross mean flight distance error of 1.26 m which is equivalent to 7.3% of speaker distance. Speaker distance (approximately 15 or 25 m) did not significantly influence performance in response to 84(-0) or 78(-0) stimuli (Fig. 5, Table 3;  $t_{12}=0.76$ , two-tailed  $P=0.46$ ).

In comparison with distances flown in response to control stimuli, subjects flew significantly greater distances in response to attenuated stimuli, 84(-6) and 84(-12), and significantly shorter distances in response to the amplified 84(+6) stimulus (Fig. 5, Table 3;  $F_{3,75}=35.17$ , one-tailed  $P<0.0001$ ). Birds also flew a significantly greater distance in response to the 84(-12) stimulus than in response to the 84(-6) stimulus (ANOVA post hoc test:  $P<0.05$ ). These results suggest a bimodal distribution of flight distances for the amplitude-altered playbacks (see below, Fig. 5).

Both 78(-0) and 84(-6) stimuli were played to subjects at 78 dB. Thus, overflight of the speaker broadcasting the 84(-6) stimulus not only demonstrates that SPL functions as a distance cue, but also that towhees estimate source SPL using at least one association with a spectrotemporal variable, that is, for example, either a decrease in call playback source SPL or an increase in call frequency and a decrease in call duration produced flight beyond the speaker location (in approximately half of the trials).

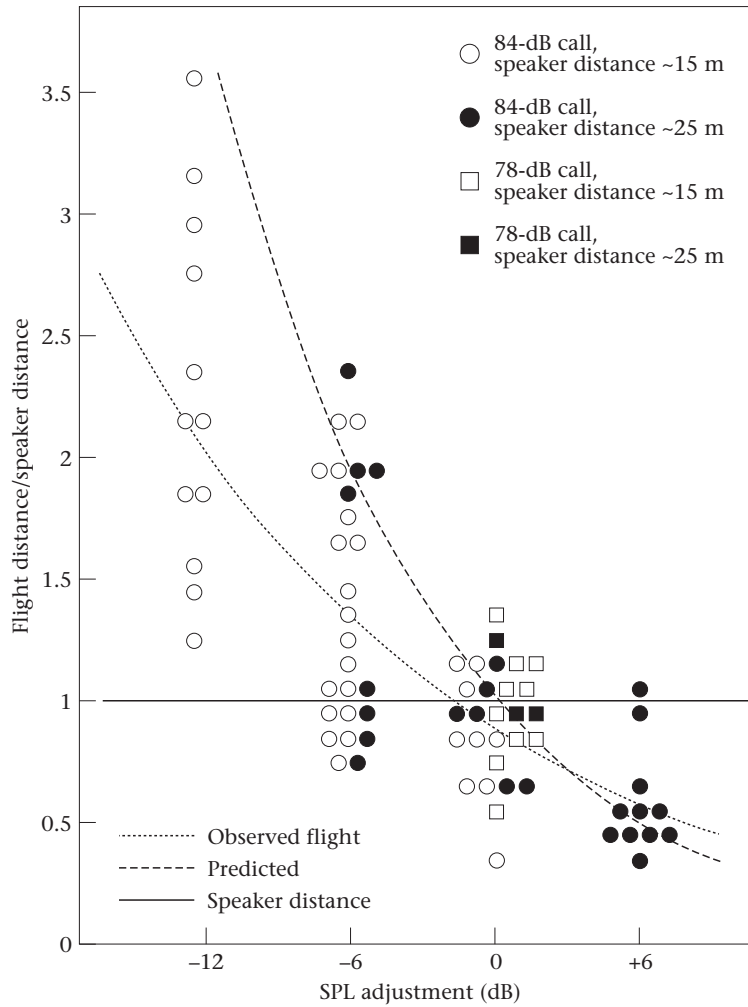
## DISCUSSION

Calls recorded from free-ranging towhees and those recorded with a microphone (Brüel & Kjaer 4189) placed 100 cm from a towhee perched on a small snag could not be distinguished from calls given by subjects in the cage. The possibility that placement in the cage influenced calling behaviour in some unknown way cannot be ruled out. However, placement in the cage is unlikely to have caused the associations described above between spectrotemporal variables and source SPL.

### Accuracy of SPL Estimation Using Spectrotemporal Variables

The reliability of SPL as a cue to auditory distance depends on the accuracy with which a listener can predict source SPL. Measurements of SPL in 1995 and 1997 varied over 26 dB (range 64–90 dB), measurements of the lowest frequency varied over 1.19 kHz (range 1.8–3.0 kHz), and measurements of highest frequency varied over 2.14 kHz (range 2.5–4.6 kHz). Birds can discriminate a 1–2% change in frequency between 1 and 5 kHz, corresponding to a 20–40-Hz change near 2.0 kHz and a 40–80-Hz change near 4.0 kHz (Dooling 1982). Thus, assuming that towhee frequency discrimination is similar to the species that have been tested, towhees should be able to estimate source SPL to within 0.5 dB under ideal conditions using spectral cues alone (e.g.  $2144 \text{ Hz}/40 \text{ Hz}=53.5 \text{ Hz}$ ;  $26 \text{ dB}/53.5 \text{ Hz}=0.49 \text{ dB}$ ). However, such a fine resolution can only occur if associations between source SPL and spectrotemporal variables are without error. To that end, a more conservative analysis can be made using measurements of standard error obtained through regression.

Measurements of standard error obtained through multiple regression suggest that using spectral cues, all individuals should be able to assess the source SPL of any single call to within  $\pm 3.7$  dB with 95% confidence (Table 1, SE=1.85,  $1.85 \text{ dB} \times 2=3.7 \text{ dB}$ ). Similarly, by listening to at least five calls from a bout, subjects should be able to assess mean source SPL to within  $\pm 2.5$  dB with 95% confidence (Table 1, SE=1.22,  $1.22 \times 2=2.44 \text{ dB}$ ). However, as explained below, these estimates may be too conservative because much of the error about regression lines can be attributed to methodological error that should not constrain a free-ranging bird's ability to predict source SPL.



**Figure 5.** Flight distance as a proportion of actual speaker distance (15 or 25 m), in response to the 84(-0), 84(-6), 84(-12), 84(+6) and 78(-0) stimuli. On average, subjects flew closest to the actual speaker location in response to 84(-0) and 78(-0) stimuli, over-flew attenuated stimuli, 84(-6) and 84(-12), and underflew amplified stimuli, 84(+6).

**Table 3.** Means±SD and sample sizes of playback trial flight distances

Stimulus	Attenuation (dB)	Absolute SPL (dB)	Speaker distance (m)	Mean±SD flight/speaker distance	N
84 (-0)	-0	84	15	0.79±0.26	8
84 (-0)	-0	84	25	0.89±0.22	6
84 (-6)	-6	78	15	1.40±0.46	18
84 (-6)	-6	78	25	1.45±0.61	8
84 (-12)	-12	72	15	2.24±0.71	12
84 (+6)	+6	90	25	0.59±0.20	11
78 (-0)	-0	78	25	1.00±0.19	14

I recorded calls with the microphone placed only 100 cm from the centre of each subject's cage (20 × 20 × 20 cm) to maximize signal-to-noise ratios and to minimize the magnitude and bandwidth of interference peaks and notches in the frequency spectrum of each recorded call. Unfortunately, a bird's movement

within the cage at this short distance (± 10% of microphone distance) produced at least ± 1 dB of overall variation about the regression lines (Table 4). Additional error, which free-ranging towhees may never or rarely encounter, can be attributed to error in analysis, error in calibration (0.3 dB for the Brüel & Kjaer 4231 acoustic

**Table 4.** Approximate and cumulative error about the regression lines explained by methodological error and the effects of this error on distance assessment

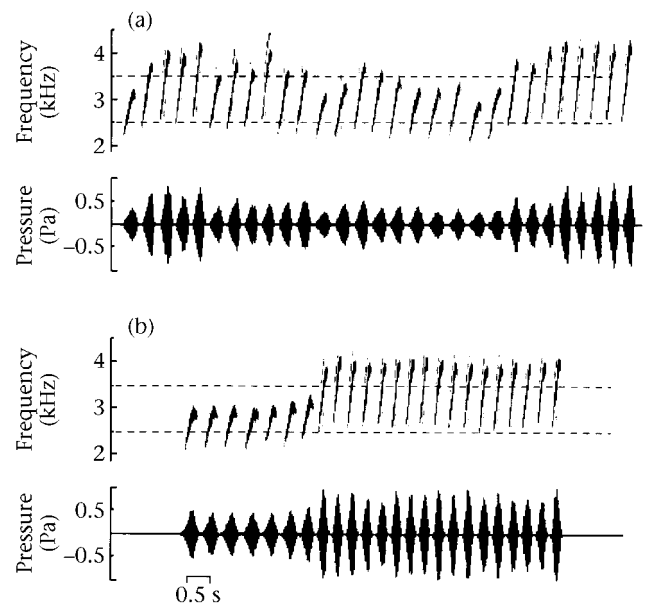
Source of measurement variation	SPL variation explained (dB)	Cumulative SPL variation explained (dB)	SPL variation remaining (dB)	Distance error due to error in SPL estimation
95% confidence*		0	±3.7	+53%, -35%
Abnormal posture, calibration, analysis, reflection from ground and/or vegetation, etc.	±0.5	±0.5	±3.2	+44%, -31%
Movement in cage	±1	±1.5	±2.2	+29%, -22%
Variation in orientation	±1.5	±3	±0.7	+8%, -8%

\*Error calculated using a 95% confidence level in a multiple regression model with the lowest and highest frequency entered as independent variables among individual calls ( $SE=1.85$ ,  $1.85 \times 2=3.7$  dB). See text for descriptions of each source of SPL measurement variation. Positive distance error represents error in distance assessment beyond the playback speaker (as a percentage of the actual source distance). Negative error represents error to the front of the playback speaker.

calibrator), variation in the location of reflective surfaces near the omnidirectional microphone and abnormal postures often assumed by subjects while calling from inside the cage (e.g. calling while perched on the side of the cage with tail and wings spread; Table 4). An approximate and conservative summation for additional error would be  $\pm 1.5$  dB (see Table 4) and, thus, the variation over which towhees may estimate call source SPL would be approximately  $\pm 2.2$  dB.

Figure 3 shows the degree to which error observed around the regression lines can be attributed to a subject's orientation relative to the microphone. Variation in orientation explains an additional  $\pm 1.5$  dB of variation about the regression lines. However, free-ranging towhees may rarely be able to determine a signaller's orientation and might also be expected to face a similar  $\pm 1.5$  dB uncertainty. For this reason, I excluded error about the regression lines due to variation in orientation in my rough estimate of error that free-ranging towhees may never or rarely encounter. However, much of the remaining variation about the regression lines not explained by methodology (Table 4) is explained by variation in the subject's orientation (see Table 4;  $\pm 3.7 - \pm 1.5$  (estimate) =  $\pm 2.2$ ;  $\pm 2.2 - \pm 1.5$  (approximate) =  $\pm 0.7$  dB). Thus, a listener's ability to assess signaller orientation may be an important factor that limits the use of SPL attenuation as an auditory distance cue.

Individual towhees in Florida do not normally give calls at a single and consistent SPL over time. Instead, any individual in the population might, over time, vary call variants and associated SPL (Fig. 6a), or repeat and switch between two or more apparent call variants and SPLs during a single bout (Fig. 6b). The eastern towhees at Archbold Biological Station are nonmigratory and defend the same territory from year to year. As a result, neighbours may be able to estimate source SPL more accurately if vocalizations of individuals are more consistent in their association between source SPL and spectrotemporal variables. I have been unable to obtain calls from subjects on more than one occasion and, as a result, I cannot analyse adequately associations with source SPL among individual calls given by single subjects.



**Figure 6.** Time spectrograms and waveforms of calls recorded from two subjects (a and b) during a single recording period with time intervals between calls removed. Calls are presented in the order in which they were recorded. Variation during each bout illustrates how any towhee in the study population might vary their calls over time.

### SPL as a Vocalization Variable

One obvious question that stems from the analyses above is why towhees vary source SPL at all. If the only explanation for the associations between spectrotemporal variables and SPL was that SPL functions as a distance cue, as I have suggested, a signaller could vocalize more easily at a single and consistent SPL.

Due to the difficulty in determining the source SPL of vocalizations given by free-ranging signallers, SPL has received little attention among bioacousticians either as an auditory distance cue or as a vocal variable available for communication. None the less, birds appear to pay attention to variation in the playback SPL of previously

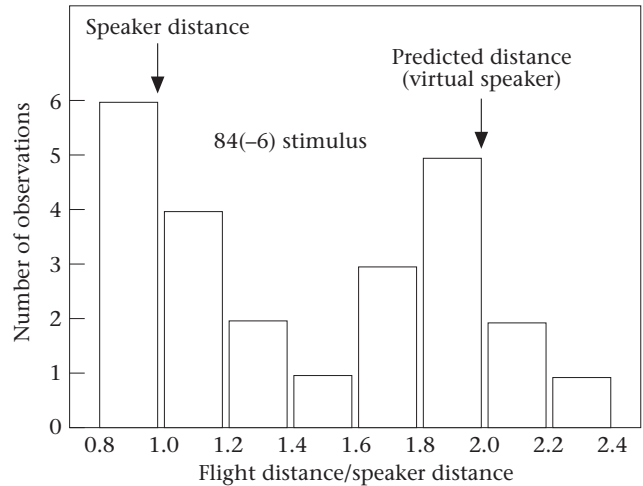


recorded conspecific vocalizations. Dabelsteen (1981) and Todt (1981) demonstrated that, relative to a 'typical' playback volume, European blackbirds, *Turdus merula*, react more aggressively, but for a shorter period, when playback volume is increased. Conversely, European blackbirds either do not react, or react less aggressively, in response to low-volume playbacks. In addition, Searcy (1996) demonstrated that female red-winged blackbirds, *Agelaius phoeniceus*, give significantly more copulation-solicitation displays in response to songs presented with greater volume. Therefore, one might not conclude on this evidence alone that SPL normally functions as a salient vocal variable because we do not yet know whether these species vary source SPL systematically during vocalization production. In this study, I demonstrate that towhees vary source SPL systematically during call production (i.e. source SPL varied systematically with spectrotemporal variables) and that towhees pay attention to this variation when estimating auditory distance.

Control of call source SPL may be important for both territory defence and predator evasion due to the direct relationship between source SPL and how far a vocalization can be expected to travel before dropping below a listener's audible threshold. A call given at a high SPL (e.g. 84 dB re 20  $\mu$ Pa) may travel across several territories and be detected several hundred metres away, whereas a call given at a low SPL (74 dB) may travel less than 100 m and go undetected by listeners beyond the signaller's territory boundary. Animals may sometimes benefit by calling as loudly as possible but may, at other times, be at a disadvantage if calling loudly attracts a predator or gains the unwanted attention of an aggressive rival (Zahavi 1979; Ryan 1988). SPL-calibrated recordings of towhees have been obtained under too few conditions to determine whether this call is an example of an 'honest signal'. It remains possible that towhees may occasionally produce calls with a higher or lower than expected source SPL (i.e. higher or lower than estimated, given correlated spectrotemporal variables) so as to sometimes appear closer or further away from listeners.

### Assessment of Auditory Distance

Ranging is a term that is commonly used to describe an animal's ability to assess distance using auditory cues (e.g. Morton 1982; Wiley 1998). Use of this term, however, appears to be based on the assumption that an animal assesses range using a single sensory modality. For example, after hearing a familiar sound, an animal might 'compute' the range of the sound source using degradation or SPL attenuation and then compare this estimate of sound source range with an estimate of distance to a biologically relevant location (e.g. the distance to a territory boundary, mate, food source, etc.). Alternatively, an animal can incorporate auditory cues, visual cues, knowledge of surrounding habitat and an estimate of sound source direction (i.e. azimuth and possibly elevation) into a single refined perception of a physical location (e.g. a location in front of a tree, but behind a small clearing of vegetation and to the left of a shrub; see Nelson & Stoddard 1998 for further discussion). The



**Figure 7.** Histogram of flights made by subjects in response to the 84(-6) stimulus. Subjects flew just short of either the actual speaker location or the predicted (virtual source) distance, but rarely flew an intermediate distance.

distinction between these two perceptual mechanisms is subtle (the distinction between an assessment of range versus an assessment of the physical location of a sound source or signaller), but important if we wish to understand the spatial cues that can be acquired from acoustic signals propagating in natural habitat.

Eastern towhees in Florida scrub habitat can use SPL as an auditory distance cue, as shown by a significant increase in distances flown in response to attenuated stimuli and a significant decrease in distances flown in response to an amplified stimulus. None the less, subjects did not always fly further in response to attenuated calls or a shorter distance in response to an amplified stimulus. This response is most evident in trials conducted with the 84(-6 dB) stimulus where most subjects flew either to the real speaker location or to the predicted (virtual source) location and rarely flew an intermediate distance (Figs 5, 7). A similar clustering of flights around both the actual speaker position and the predicted (virtual source) distance was observed by Nelson & Stoddard (1998). In that study, stimuli were degraded artificially and attenuated individually to represent an intruder located two or three times further than actual speaker distance. Taken together, these two experiments suggest that degradation cues found to be important in other studies (e.g. Richards 1981; Morton 1982; McGregor 1994; Naguib 1998), are probably less important for towhees in Florida scrub habitat over the distances tested in this study. Components of degradation may become more salient over distances greater than 40 m and towhees may rely differentially on an auditory assessment of range over these longer distances.

Several factors may account for the highly variable distances flown in response to the 84(-12) call stimulus (Fig. 5). A 12-dB decrease in SPL corresponds to a four-fold increase in linear distance, assuming sound attenuates at a rate of -6 dB per doubling of distance (~60 m). Therefore, subjects may have flown an unpredictable

distance because the simulated territory intruder may have been perceived as near or beyond the subject's territory boundary. Towhee territories are highly variable in size (Greenlaw 1996), but generally have diameters of ~70–100 m at Archbold Biological Station. Alternatively, subjects may have varied their flight distance due to uncertainty in the function with which sound attenuates over long distances in Florida scrub habitat. More likely, however, the discrepancy between two potential sound source locations (i.e. the actual speaker's location or a location approximately four times as far) was so great that subjects chose to fly an arbitrary distance towards their territory boundary, perhaps in an attempt to locate visually a territorial intruder in the speaker's direction or to hear another call at a closer range.

### Implications for Other Species and More Complex Vocalization

Due to the difficulty involved in determining the source SPL of vocalizations given by free-ranging signalers, researchers have had few opportunities to look for associations with source SPL or determine whether other species can estimate source SPL when variable. Humans convey greater vocal effort (i.e. stress or expression) by increasing source SPL and this increase in source SPL is associated with spectrotemporal variation (i.e. frequency bandwidth increases and duration measurements most often decrease as source SPL increases; Brandt & Kenneth 1969; Glave & Rietveld 1975; Sluifjter et al. 1997). In addition, SPL is a salient distance cue for humans in open nonreverberant environments (Mershon & King 1975; Nielsen 1993), and humans are able to assess vocal effort despite substantial variation among individual speakers. While not yet explicitly tested, these behaviours suggest that humans might also often estimate source SPL using spectrotemporal variation.

Additional behaviours or environmental conditions might also be associated predictably with variation in source SPL. For example, zebra finches, *Taeniopygia guttata* (Cynx et al. 1998), and budgerigars, *Melopsittacus undulatus* (Manabe et al. 1998), have been found to correlate variation in source SPL with variation in background noise level under laboratory conditions.

Subjects in my playback experiments appeared to be 'familiar' with the associations I describe, as demonstrated by a dependence on the estimation of source SPL for accurate speaker localization. It remains unclear whether 'familiarity' exists due to learning or as a result of an innate or physical coordination between perception and production. None the less, these results seem to support earlier contentions that assessment of distance is, in part, dependent on familiarity (Morton 1982, 1998). Half of the subjects in this study, as well as in an earlier study (Nelson & Stoddard 1998), were able to assess accurately speaker locations despite experimental variation of source SPL. Thus, familiarity does not appear to be a prerequisite for accurate localization.

Birds commonly give simple calls. None the less, literature on avian auditory distance perception is dominated by investigations concerned primarily with the

perception of acoustically more complex 'song'. Avian song is highly variable, but often consists of at least one repeated element or note. Thus, unless the associations between the source SPL and the spectrotemporal variables I describe are unique to this eastern towhee vocalization, redundancy in acoustically more complex 'song' should allow for a more refined estimation of source SPL and subsequent assessment of auditory distance under comparable acoustic conditions.

### Acknowledgments

I thank P. K. Stoddard for help during all phases of this research, M. Donnelly, J. Hailman, J. Heinen, M. Naguib, C. L. Pytte, W. A. Searcy, R. A. Suthers, K. Tarvin and several anonymous referees for helpful comments on the manuscript. Support and equipment was provided by Archbold Biological Station, Florida International University, Brüel & Kjaer and the Eastern Bird Banding Association. The research presented here was reviewed by the Animal Behavior Society Animal Care Committee and approved on 31 March 1999.

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