Accuracy of auditory distance and azimuth perception by a passerine bird in natural habitat

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ABSTRACT

Small birds should localize sound poorly because small head size limits azimuth resolution and because the loose correlation of acoustic degradation with distance limits accurate estimation of auditory distance. We determined the accuracy of sound localization by a passerine bird in the field using an open-loop phonotaxis experiment. After hearing a playback of a conspecific contact call, eastern towhees, *Pipilo erythrophthalmus*, approached the silenced source. Mean auditory distance resolution was 7% of total speaker distance and mean azimuth resolution was $\pm 5°$. In a second experiment, we played birds the same calls rerecorded previously over the 10- or 20-m distance beyond each playback location. In 13 of 30 trials, the birds over-flew the speaker by a distance propotional to rerecording; but in 15 trials, approach distances were comparable to speaker distance despite the addition of distance simulated by attenuating and rerecording the calls. Signal-specific and location-specific distance cues are derived to explain the bimodal distribution of flight distances we observed.

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To determine the location of a sound source, an animal determines the sound's azimuth, elevation and distance. Auditory resolution of azimuth and elevation are the result of interaural time differences and monoaural amplitude cues (e.g. Carr & Konishi 1990; Konishi 1993). Studies have shown that playback of bird song with attenuated high frequencies or addition of reverberation produces behaviour consistent with the perception of increased auditory distance (Richards 1981; McGregor 1994; Naguib 1996, 1997; Wiley & Godard 1996). Compared to our understanding of angular resolution, however, we know relatively little about the accuracy and specific mechanisms underlying perception of auditory distance.
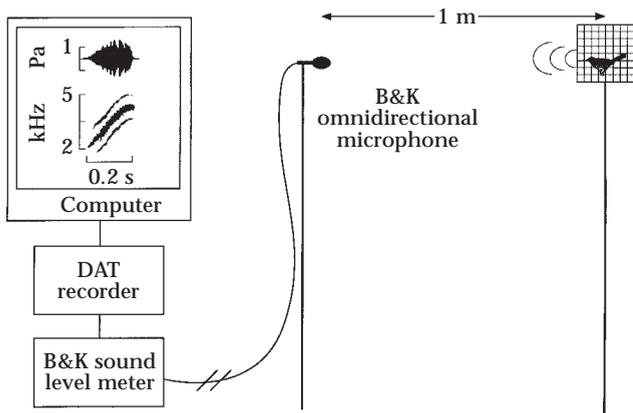
Small birds are interesting subjects for sound localization experiments because, although accurate localization is behaviourally important, small head size seems to preclude accurate sound localization (Klump et al. 1986; Park & Dooling 1991; Klump & Larsen 1992). Small birds in the laboratory resolve auditory azimuth to about a 25° minimum resolvable angle in speaker choice tests (Park & Dooling 1991; Klump 1996b). Conversely, vertebrates with larger heads, such as humans, and some sound localization specialists such as owls and harriers,

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resolve auditory azimuth to within 1–2° under laboratory conditions (reviewed by Rice 1982; Brown & May 1990).

Studies of auditory distance perception have focused on the relevant cues used by birds and humans to assess auditory distance (Mershon & Bowers 1979; Brown & May 1990; McGregor 1994). Only one study to date has explored the accuracy of auditory distance resolution in birds. Konishi (1973) tested the ability of barn owls, *Tyto alba*, to hit a simulated mouse target 2 m away. If he turned off the speaker when the owl left the perch, the owl's mean strike error was ± 20 cm, or 10% of the sound's distance distributed symmetrically around the speaker. Naguib (1996) also measured flight distance of territorial male Carolina wrens, *Thryothorus ludovicianus*, in response to playback of normal and distance-degraded songs; but, he reported speaker overflight and underflight distances separately, so we cannot use his data to assess the accuracy of phonotaxis by Carolina wrens. Presumably his raw data could be reanalysed to extract information on quantitative accuracy of phonotaxis.

Humans are reported to progressively underestimate perceived distance as actual distance increases (Coleman 1963), although these studies have been criticized for using biased methods (Mershon & King 1975). The literature on human performance points out the importance of acoustic environment. The mechanisms and accuracy of auditory distance resolution in humans is reported to differ between acoustic environments, for example, in a
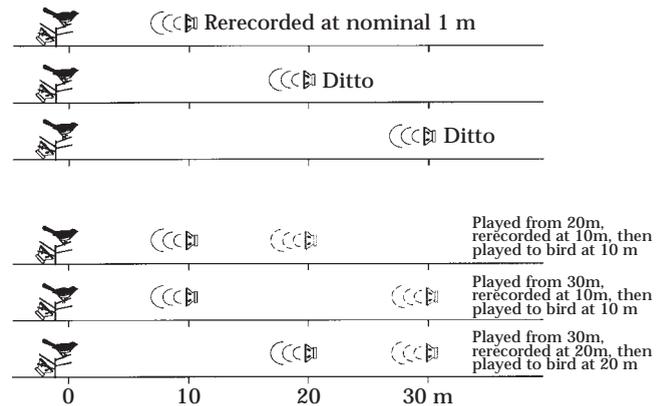
Figure 1. Towhee calls were recorded from birds placed in a 20-cm³ wire cage atop a 1.25-m pole. Recordings were made using an omnidirectional microphone 1 m from the cage. Birds did not always face the microphone, but orientation only affected recording SPL by a maximum of ±2 dB (B. S. Nelson, unpublished data). The inset shows time∗amplitude waveform and time spectrogram of a typical towhee call used as a stimulus.

Figure 2. Each towhee subject received six playback trials on different days and in random order. In three trials, the call, rerecorded at a nominal distance of 1 m from the microphone, was played approximately 10, 20, or 30 m from the towhee on the starting perch. In two trials, calls rerecorded 10 or 20 m from the microphone were played to the towhee from 10 m. In one trial, the call was rerecorded 10 m from the microphone and played to the towhee from 20 m.

reverberant room versus an anechoic chamber (Mershon & King 1975; Mershon & Bowers 1979; Nielsen 1993). Sensory mechanisms of sound localization evolved in complex outdoor environments, not in reverberant rooms or anechoic chambers, so we are not confident that laboratory studies always make the preferred acoustic cues available to the subjects.

We conducted a field experiment on the accuracy of sound localization by free-living, territorial passerine birds using a phonotaxis design most similar to a design used with barn owls and frogs in a laboratory setting (Konishi 1973; Klump 1996c). We chose as our subject males of the eastern towhee, *Pipilo erythrophthalmus* (Passeriformes, Emberizidae), living in the dense oak and pine scrub of the Lake Wales Ridge of central Florida (Abrahamson et al. 1984). Male eastern towhees are good subjects for a phonotaxis experiment because they are strongly territorial and readily attack a playback speaker. Towhees on our site must rely heavily on auditory cues to locate mates and territorial intruders because the Lake Wales scrub habitat is extremely dense.

We lured territorial male towhees to predetermined starting perches in their territories using the playback of conspecific vocalizations that differed from those used as stimuli. We then played a prerecorded towhee call (e.g. Fig. 1) from a concealed speaker 10, 20 or 30 m away but within the subject's defended territory, stopping playback when the subject took flight (Fig. 2). We noted the subject's perch positions as it attempted in vain to locate the simulated intruder. After each trial ended, we measured flight distances from the starting perch to each landing perch, and perpendicular distance from each landing perch to the axis between starting perch and the playback speaker.

Numerous playback studies with territorial male passerine birds have shown that response to playback of a conspecific vocalization is less aggressive if the stimulus is previously degraded by rerecording over a distance. These data have been interpreted as evidence that sound degradation increases perceived auditory distance (reviewed by McGregor 1994). Because our procedure is a direct assay of perceived auditory distance, in contrast to the indirect assays used previously, we considered it important to run some trials using stimuli rerecorded over a distance beyond the playback speaker. So, mixed in with the 10-, 20- and 30-m trials described above, we conducted trials with experimental calls previously rerecorded over the 10- and 20-m distances beyond the 10-m speaker locations, and with calls rerecorded over the 10-m distance beyond the 20-m speaker positions (Figs 3, 4). For these trials we set sound pressure level (SPL) at the receiver to approximate that heard if the caller were vocalizing at the distance equal to the sum of the playback distance and the rerecording distance (see below).
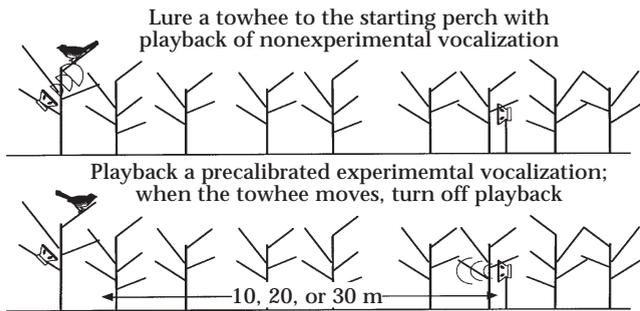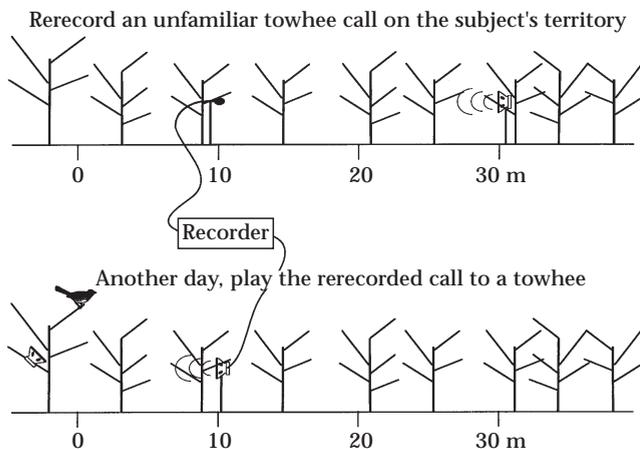
METHODS

Subjects

We selected 10 male towhees as subjects from sites over 5 km from the territories of the birds whose calls we used as stimuli. A towhee was selected if he frequented a conspicuous perch near his territory boundary that could be used as a starting perch during the playback trials. Four of these birds defended territories in long unburned sand pine scrub, and six defended territories in scrubby flatwoods burned within the past 5 years (Abrahamson et al. 1984).

Playback Stimuli

We chose as stimuli one call recorded from each of 10 additional colour-banded eastern towhees that defended territories throughout a 10-km² area of the Archbold Biological Station, 12 km south of Lake Placid, Florida, in May–July 1995. Mist-netted male towhees readily called

Lure a towhee to the starting perch with
playback of nonexperimental vocalization

Playback a precalibrated experimemtal vocalization;
when the towhee moves, turn off playback

—10, 20, or 30 m—

Figure 3. A male towhee was lured to a predetermined spot on the periphery of his territory by playing a conspecific vocalization (call or song) not used as a playback stimulus. The experimental stimulus, a prerecorded contact call, was played from a concealed speaker 10, 20 or 30 m away. When the bird moved, the speaker was turned off and the birds position noted as he attempted to locate the now silent simulated intruder.

Rerecord an unfamiliar towhee call on the subject's territory

0   10   20   30 m

Recorder

Another day, play the rerecorded call to a towhee

0   10   20   30 m

Figure 4. Calls were rerecorded for playback to simulate distance as was done in other studies. In the example shown here, a towhee call was played from the 30-m location and recorded at the 10-m location. Another day, the rerecorded call would be played from the 10-m location to a towhee positioned at the starting perch. Our question is whether the towhee would fly to the virtual source at 30 m, the real source at 10 m, or somewhere in between. Each playback call was rerecorded at 1, 10 and 20 m.

Table 1. Mean (±SD) of net and gross distance error about playback speakers (N=10 per row)

Mean speaker distance (m)	Gross distance error (m)	Net distance error (m)*	Net distance error as % speaker distance
10.19	2.30±2.04	0.67±0.41	6.58±4.02
19.79	3.54±1.74	1.91±0.11	9.65±0.56
30.76	3.42±3.06	1.79±1.43	5.82±4.65
All trials	3.09±2.33	1.46±0.70	7.35±3.08

*Net error is adjusted for perch discontinuity in natural habitat.

Table 2. Mean (±SD) of maximum flight distances from the starting perch (N=10 per condition)

Mean speaker distance [rerecording distance]	Gross distance error (m)	Net distance error (m)*
10.19 [1]	11.95±2.97	1.76±2.56
19.79 [1]	20.39±4.20	0.60±4.07
30.76 [1]	31.38±4.98	0.62±4.68
All [1] above		0.99±3.78
9.99 [10]	16.91±6.15	6.92±6.22
10.13 [20]	23.81±9.26	13.68±9.44
19.68 [10]	21.91±5.79	2.23±5.45

*Net error is adjusted for perch discontinuity in natural habitat.

when left for a few minutes in a 20-cm³ wire cage atop a 1.25-m aluminium pole (1.5 cm in diameter) situated near the middle of their territories. Calls given from the cage were indistinguishable from calls given during natural territorial interactions (B. S. Nelson, unpublished data).

We made all recordings with SPL-calibrated equipment to enable us to reproduce the original SPL of recorded calls during playback. We obtained recordings of measured SPL by placing a calibrated 0.5 inch free-field omnidirectional microphone (Brüel & Kjaer 4188) 1 m from the centre of the cage and 1.25 m above the ground (Fig. 1). Signals were amplified with a sound level meter (Brüel & Kjaer 2236) situated 20 m away and recorded onto a digital audio tape recorder (Sony TCD-D3). We recorded the reference tone from an acoustic calibrator (Brüel & Kjaer 4231) before and after each recording

period to facilitate subsequent playback at the original call amplitude (B. S. Nelson, unpublished data). We used a free-field omnidirectional microphone (Brüel & Kjaer 4188) with well-documented frequency response and directional reception pattern to ensure that all possible distance cues from reflections were embedded in our recordings; a directional microphone attenuates reception of indirect sound pathways. The 1 inch dome speaker that we used for playback (Polk Audio MM 3000) is also nearly omnidirectional, producing a sound field similar to those observed around heads of other small birds (Witkin 1977; Hunter et al. 1986; Larsen & Dabelsteen 1990). We chose an omnidirectional speaker to reproduce reverberant sound fields that would exist if an actual bird were calling from each speaker location.

To produce stimuli for playback, each of the 10 stimulus calls was rerecorded over three distances (1, 10 and 20 m) at four locations (Figs 3 and 4, Tables 1 and 2): (1) at a nominal distance of 1 m for playback at 10, 20 and 30 m (i.e. conditions 10[1], 20[1] and 30[1], respectively); (2) at a distance of 10 m over terrain directly behind a speaker positioned 10 m from the starting perch (condition 10[10]); (3) at a distance of 20 m over terrain directly behind a speaker positioned 10 m from the starting perch (condition 10[20], Fig. 3); and (4) at a distance of 10 m over terrain directly behind a speaker positioned 20 m from the starting perch (condition 20[10]). We carried out this procedure on each of the 10 playback territories to

ensure that the habitat cues embedded in the recording were correct for each playback trial.

We played calls approximately 12 dB above their original source amplitude for rerecording to maintain a signal-to-noise ratio of at least 30 dB ($\bar{X} \pm$ SD signal-to-noise ratio for calls rerecorded at 20 m=41.4 ± 6.4 dB RMS SPL, 1–5 kHz, re 20 μPa). We adjusted playback amplitude of stimuli rerecorded at a nominal distance of 1 m to levels predicted using a multiple linear regression equation with lowest frequency and frequency at peak amplitude as independent variables (B. S. Nelson, unpublished data). For the more distantly rerecorded calls, we adjusted RMS SPL to match a call played over the distance being simulated. We calibrated call SPL for playback by digital adjustment of RMS playback amplitude relative to a standardized synthetic towhee call (a computer-generated 2.0–4.0 kHz linear frequency sweep), 94 ± 0.2 dB 1 m away (RMS re 20 μPa).

We played calls from a digital tape recorder (Sony TCD-D3) when rerecording them for use as stimuli, but played them from a portable microcomputer (Apple Macintosh PowerBook 5300c) during playback trials. Signals were high-pass filtered (1.5 kHz, − 12 dB/octave) amplified, and played using an electronic crossover (Pioneer CD-635), power amplifier (Soundstream D200) and 1 inch dome speaker (Polk Audio MM 3000) oriented 45° upward. The speaker was only 4 cm across and seemed to go unnoticed by the birds. We recorded playback calls much as we did those of live birds in the cages. We placed the speaker 80–110 cm above the ground, depending on the mean vegetation height at each distance. We placed the microphone near the starting perch when measuring SPL for playback, and along a direct path between starting perch and speaker position when re-recording experimental signals. We recorded signals with a free-field omnidirectional microphone (Brüel & Kjaer 4188) connected to a 20-m extension cable to a sound level meter (Brüel & Kjaer 2236).

Playback Protocol

Each subject received six playbacks (Fig. 4) presented in random order over 2 weeks in June and July 1996. In three of these six playback trials, we played an identical call at 10, 20 and 30 m along a single axis from a single starting perch and in three trials we played experimental versions of this same call, previously rerecorded over 10 or 20 m behind the speaker. We placed a speaker near the starting perch, somewhere near the territory boundary, and attracted the subject to it by playing songs or calls not used as experimental stimuli (Fig. 2). Once a subject perched within ~1 m of the starting perch, we played a stimulus call approximately every 4 s from a second playback speaker positioned 10, 20 or 30 m away along a single axis towards the territory centre (Fig. 4). To prevent the possibilities of triangulation on the sound source or in-flight correction (e.g. Konishi 1973), we terminated playback the instant the subject moved more than 1 m horizontal or 1 m vertical from his original perch.
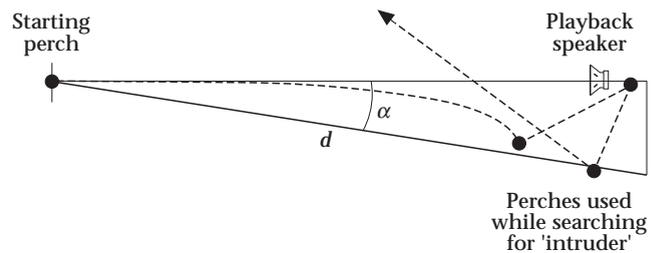

Figure 5. During a playback trial, each of the towhee's perches was recorded and measured. Furthest flight distance, d, was taken as the towhee's estimate of speaker distance, and α, the angle between that point and the speaker–starting perch axis, was taken as the towhees estimate of speaker azimuth.

Data Analysis

During a trial, we noted the bird's perch locations as the distance and direction from natural markers such as a broken branch or discoloured leaf. We transcribed and measured these locations immediately after the trial. We recorded all perch locations, but chose as a single measure of flight distance his furthest perch from the starting perch (Fig. 5) because a bird approaching a natural intruder often flies slightly short of the intruder and completes the final approach with several shorter flights. We calculated flight azimuth for all perch locations using arcsine(P/r) where P is the perpendicular distance from the axis between starting perch and the playback speaker location to each perch, and r is the distance to each perch from the starting perch.

Suitable perches are not distributed uniformly in natural habitats so accuracy of behavioural phonotaxis is limited by perch discontinuity. We can refine our estimates of perceptual accuracy by subtracting the perch distribution error from the observed error in distribution of distances or azimuths flown. While approaching a playback location, birds often made one long flight, followed by several shorter flights between adjacent perches. Perches chosen during playback response, after the initial approach flight, were distributed by a mean (± SD) distance of 3.25 ± 3.64 m (N=47) and a mean (± SD) azimuth of 7.26° ± 7.85° (N=47). Interperch distance was calculated as the difference between successive measurements of distance along each individual flight path, and interperch azimuth was calculated as the difference between successive measurements of azimuth or as a sum of successive azimuth measurements if the bird flew across the axis between the initial perch and playback speaker. Assuming that perches are distributed normally around the perceived sound source, then half of the mean interperch distance, 1.63 m, and half of the mean interperch azimuth error, 3.63°, represent mean error due to discontinuity of perches. Subtracting these quantities from the raw behavioural means allows us to estimate the perceptual capabilities underlying performance.

RESULTS

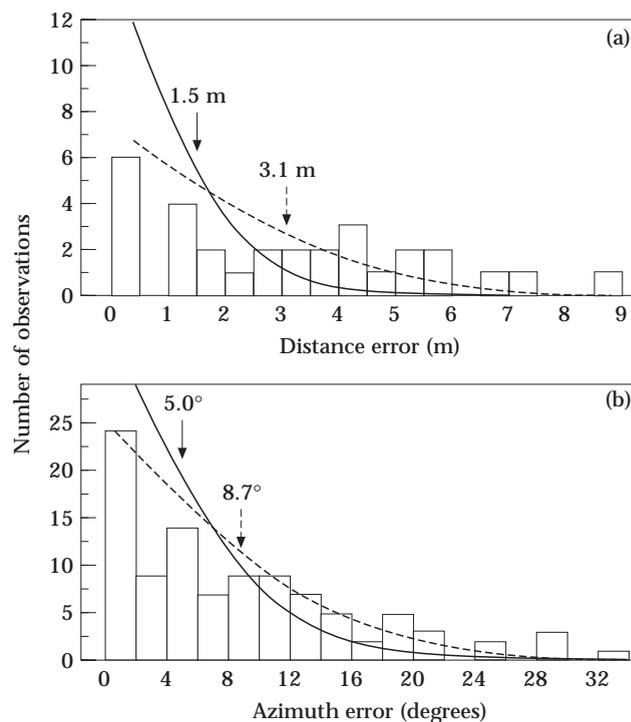Birds took flight after 1–20 playback calls, but neither the number of calls played before flight nor the order of
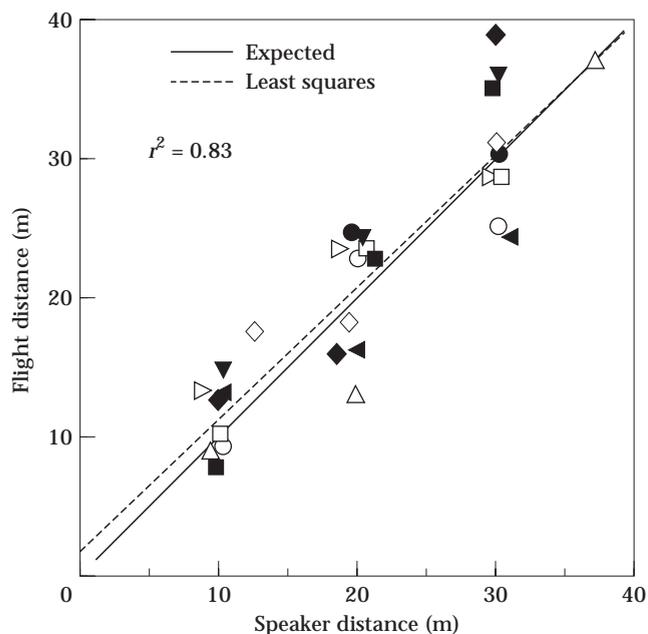
Figure 6. Scatter plot of flight distance in response to calls rerecorded at a nominal distance of 1 m and presented at ~10, ~20 and ~30 m. Birds flew close to the playback speaker with normally distributed error. Each of the 10 birds is represented by a different symbol. Symbols are spread across the *X*-axis because optimal speaker placement was not always exactly 10, 20, or 30 m.

Figure 7. Frequency distribution of (a) flight distance error (*N*=30) and (b) flight azimuth error observed during trials (*N*=100). The solid-lined curves show normalized distance error in which a normal curve is fitted to the flight distance data (a) and azimuth data (b). The dashed curves show normalized distance and azimuth error adjusted for discontinuous perch distribution by subtracting the normal curves for perch distribution distance and azimuth from the normal curves for flight distance and azimuth. Arrows indicate the mean errors for raw data and adjusted normal curves (i.e. the points representing 50% of the area under the normal curve).

playback had any statistical effect on flight distance or azimuth. Throughout the experiment, the birds stayed in a horizontal plane about 2 ± 1 m deep. Mean ($\pm$ SD) height of starting perches was 2.4 ± 1.1 m and landing perches were similar.

Distance

Furthest flight distances approximated closely the playback distances (Fig. 6; $R^2_{adj}=0.82$, SE=3.66 m, $N=30$, $P<0.0001$). Subjects approached the speaker with a gross mean flight distance error of 3.09 m, 1.46 m corrected for perch discontinuity (Fig. 7a, Table 1). After correction for perch discontinuity, mean distance error was 7.35% of speaker distance, or 7.35 cm/m. Flight distance appears to be proportional to distance, but raw flight distance errors cannot be expressed meaningfully as a percentage of speaker distance because perch mean distribution error (1.63 m) is independent of playback distance and is equivalent in magnitude to the residual error attributable to perception of distance (mean 1.46 m).

On average, towhees flew further in response to experimentally rerecorded stimuli (Fig. 8, Table 2, MANOVA: $F_{8,2}=10.09$, $P=0.001$) and flew further as rerecording distance increased behind each speaker position (ANOVA post hoc test: $P<0.05$). However, subjects did not always fly further in response to calls previously rerecorded at a distance. In our trials with rerecorded stimuli, birds appeared to fly either to the real speaker or to the virtual speaker, the latter a distance equal to the sum of the real speaker distance and the rerecording distance. This effect

was most convincing in the 10[20] condition, where the difference between real and virtual speakers was greatest (Fig. 8).

To determine whether flight distances best fit the true speaker distance or the virtual speaker distance (speaker distance plus rerecording distance), we compared actual flight distances to estimated 95% prediction intervals (boxes in Fig. 8). We calculated these intervals from the regression residuals of flight distances in the 30 trials shown in Fig. 6. The stimuli in those trials were rerecorded at a nominal distance of 1 m. Thus, 95% of flights made by birds attempting to locate a perceived sound source (either the real speaker or the virtual speaker) should fall between the upper and lower bounds of this interval plotted around the expected distance. Of the 30 flights made in response to calls rerecorded 10 or 20 m beyond the speaker, approximately half fell within the 95% prediction interval plotted around the true speaker distance (rectangular boxes in Fig. 8) and half fell within the same interval plotted around the virtual speaker distance (slanted boxes in Fig. 8). The paucity of flight distances in the zone between the 95% intervals around the real and virtual speaker distances supports our interpretation of a split distribution in perceived speaker distance. Individual birds were not consistent in their
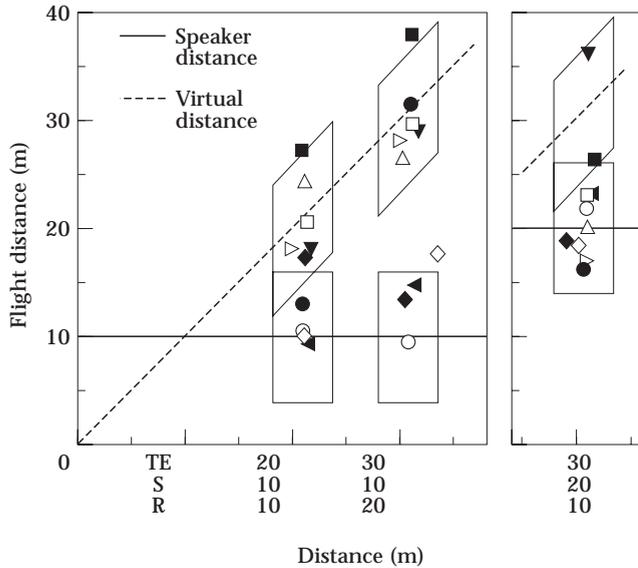
Figure 8. Flight distance in response to calls rerecorded 10 m behind 10-m and 20-m speaker positions or 20 m behind 10-m speaker positions. TE: total emulated distance; S: speaker distance; R: rerecording distance. Thin-lined boxes are 95% prediction intervals derived from the distribution of flights in response to playback calls prerecorded from 1 m away (data shown in Fig. 6). If birds were flying exclusively to the actual playback speaker, 95% of flights should fall within the rectangular boxes. If birds were flying to the virtual speaker (sum of playback and rerecording distances), 95% of flights should fall within the diagonal boxes. In 13 of 30 trials, birds flew beyond the playback speaker a distance proportional to rerecording distance (i.e. to the virtual sound source). In 15 of 30 trials, birds flew a distance comparable to speaker distance, disregarding the added virtual distance embedded in the rerecording. Only 2 of 30 flights fell outside the 95% prediction boxes and only 1 flight was in between.

choice between the actual and virtual speaker distances. A bird that flew the shorter distance in one trial (e.g. flew ~10 m in the 10[20] trial) was just as likely to fly the longer distance in the other trial (e.g. fly ~30 m in the 20[10] trial).

Azimuth

Subjects resolved speaker azimuth with a gross mean error of 8.7° among all trials, 5.1° corrected for perch discontinuity (Fig. 7b, Table 3). Azimuth resolution lost no accuracy as flight distance increased in trials with stimuli rerecorded at a distance (Table 1; r^2_{adj}= 0.027, SE=7.61 m, P<0.15).

DISCUSSION

Perception of Auditory Distance

Towhee distance perception was accurate to within ± 7% over 10–30 m (Tables 1 and 2). In a similar experiment, a captive barn owl showed a mean accuracy of ± 10% over a 2-m distance (Konishi 1973). Playback trials with stimuli rerecorded over 10 or 20 m give us some

Table 3. Mean (±SD) of lateral perch error (N=10 per condition)

Mean speaker distance (m) [rerecording distance]	Gross perpendicular distance (m)	Gross azimuth error (°)	Net azimuth error (°)*
10.19 [1]	1.43±1.00	8.57±7.83	4.94±4.20
19.79 [1]	4.10±3.41	12.28±9.50	8.65±5.87
30.76 [1]	3.45±3.48	7.56±7.68	3.93±4.05
All [1] above	3.04±3.08	9.40±8.44	5.77±4.81
9.99 [10]	1.83±1.45	7.75±5.51	4.12±1.88
10.13 [20]	2.89±3.73	8.17±7.37	4.54±3.74
19.68 [10]	2.69±2.81	8.11±7.75	4.48±4.12
All trials	2.77±2.96	8.70±7.68	5.07±4.05

*Net error is adjusted for perch discontinuity in natural habitat.

hints as to the cues towhees use in determining auditory distance. In about half of these trials towhees flew to the virtual sound source, a distance equal to the sum of the speaker distance and the rerecording distance. In the remaining trials, the birds flew close to the actual playback speakers. That the birds were fooled by the rerecording half the time indicates that they attend to sound amplitude and/or some other cues to distance that are affected by rerecording. That the birds were not fooled by the rerecording the rest of the time indicates that they also attend to another distance cue as yet undescribed.

In human listeners, the ratio of direct to reverberant sound has been implicated as a cue to auditory distance (Mershon & King 1975). In studies of passerine auditory distance perception, inclusion of artificial reverberation by rerecording in an attic produced a significant drop in territorial behaviour and increase in flight distance consistent with perception of increased playback distance (Naguib 1995, 1997). We attempted to capture natural reverberation in our rerecordings by rerecording at each site where trials were conducted and by using an omnidirectional microphone and speaker. Yet our birds located the actual playback speaker in about half of the trials with stimuli rerecorded 10 or 20 m away.

Auditory Distance Cue Models

To explain the bimodal distribution of flights we observed, we consider two types of auditory distance cues; signal-specific cues and location-specific cues. Signal-specific cues (relative cues) require prior knowledge of an original signal and can be encoded in both direct sound and a monaural playback. Location-specific cues (absolute cues), in contrast, require no prior knowledge of the original signal and cannot be encoded realistically in a monaural playback.

Signal-specific Cues

We consider five signal-specific cues; overall amplitude of direct sound, frequency spectrum of direct sound,
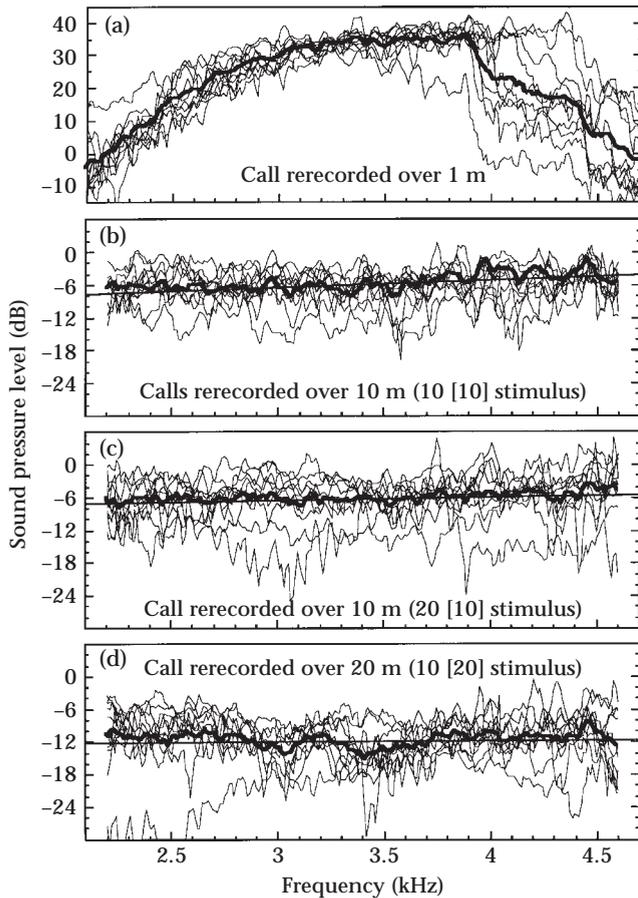
Figure 9. (a) Individual spectra (thin lines), mean spectrum (thick line) and linear regression (straight thin line) of the 10 control stimuli. (b–d) The spectral effects of rerecording experimental stimuli at a distance, as determined by subtracting each spectrum of a stimulus rerecorded at a distance (10 or 20 m) from its corresponding 1-m spectrum in (a). Mean SPL did not decrease predictably with frequency as measured over long distances in different field habitats (Marten & Marler 1977; Wiley & Richards 1978), indicating that differential attenuation of high frequencies could not have been a cue to auditory distance in this experiment.

overall amplitude of reverberation, frequency spectrum of reverberation and acoustic degradation.

Overall amplitude of direct sound

Overall amplitude of direct sound decreases inversely with distance. Towhees can predict source amplitude from call spectro-temporal variables and use a decrease in overall incident amplitude as a cue to auditory distance (B. S. Nelson, unpublished data). Decreases in call playback amplitude probably led to perception of greater distance and to flight beyond the playback speaker in this experiment as well.

Frequency spectrum of direct sound

Frequency spectrum of direct sound may be useful as an auditory distance cue when related to distance in a predictable manner. We did not find a predictable shift in call frequency spectrum over the frequency range spanned by the towhee's call (~2.5–4.5 kHz, Fig. 9),

but Naguib (1995) presents evidence that frequency-dependent attenuation is used for ranging by the Carolina wren in a woodland habitat.

Acoustic degradation

Monaurally received sound is comprised of direct sound and time-delayed reverberation. As the distance from the sound source increases, the ratio of direct to reverberant sound decreases, and therefore, the ratio may convey distance when it changes in a predictable manner (Dabelsteen et al. 1993, 1997). However, because birds may accurately perceive azimuth (in this study we show that the towhee perceives azimuth to within 5°) and because echoes arrive after a time delay, we argue that birds may often be able to resolve echoes separately from direct sound. In place of degradation, we propose two signal-specific cues (overall amplitude and frequency spectrum of reverberant sound) and two location-specific cues to explain better our results with the towhee (see below).

Diffuse reflected sound of random orientation is operationally defined as reverberation. Reflected sounds discriminably louder than background reverberation and temporally distinct from the direct sound are defined as echo (White 1987).

Overall amplitude of reverberation

Overall amplitude of reverberation decreases inversely with distance and towhees may use a decrease in overall reverberation amplitude as a cue to auditory distance (just as overall amplitude of direct sound is used as a distance cue).

Frequency spectrum of reverberation

Frequency spectrum of reverberation may also be useful as an auditory distance cue when related to distance in a predictable manner (just as frequency spectrum of direct sound may sometimes be used as a distance cue).

Reflected sound with adequate time delay (time delay <10 ms in Fig. 10) will arrive after a brief period of early reflection from objects near the path of direct sound (time delay <10 ms in Fig. 10) and after early reflection from the ground (time delay <10 ms in Fig. 11, although the exact time delay will depend on a source's height above the ground). Echoes arriving within 5–10 ms of the direct sound can either be disregarded or suppressed (Keller & Takahashi 1996). In either case, as distance increases, those echoes and the reverberation with an amplitude and frequency spectrum most highly correlated with sound source distance (time delay >10 ms in Figs 10, 11) will arrive increasingly from behind the sound source.

Location-specific Cues

We describe two novel location-specific cues, off-axis reflection and near-axis reflection, and a previously proposed cue, elevation of direct sound.
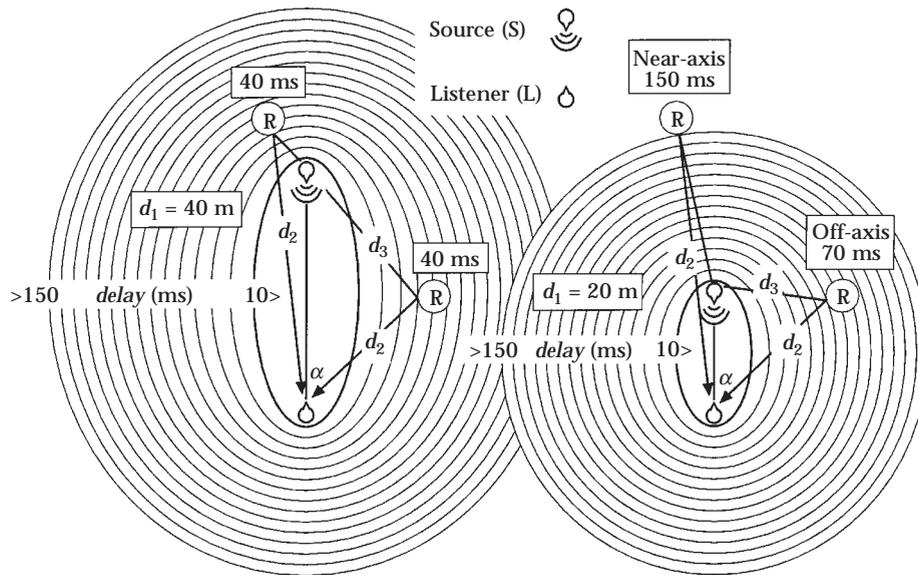
Figure 10. For simplicity, these illustrations consider only initial reflection that will arrive at the listener (L) with the greatest amplitude. Off-axis echo cue to distance; the illustration depicts both the path taken by direct sound (d_1) to reach a listener (L) located 20 or 40 m from a sound source (S) and the indirect path (d_2 and d_3) taken for reflected sound to reach the same location when reflected by an off-axis object (R). The concentric ellipses represent the locations of potentially reflective points producing equal delay. Echo following the indirect path will reach the listener's location (L) after a 40-ms delay when the listener is 40 m away, and after a 70-ms delay when the listener is 20 m away. When a listener can identify and assess both the distance to a discrete off-axis reflector (R) and the angle between the reflector and the sound (α) source, delay can be used to determine distance to the sound source (d_1). Near-axis echo cue to distance; objects more or less in line with the direct sound path maximize the effect of source distance on echo delay and simplify the calculations required to determine the source distance (d_1) from echo delay. An echo off the reflector (R) will reach the listener's location (L) after a 40-ms delay when the listener is 40 m away and after a 150-ms delay when the listener is 20 m away.

Off-axis reflection

Assume a sound source S and a listener L some distance d_1 apart (Fig. 10). Somewhere to the side is a reflective object R such that d_2 is the distance from R to L, and d_3 is the distance from S to R. Sound travels from S to L along a direct path of length d_1, and along an indirect path, reflected off R, of length d_2+d_3. The angle between the direct and indirect (reflected) sound paths arriving at the listener is α. The delay between arrival times of the direct and indirect sounds equals the difference in path lengths divided by the speed of sound in air (344 m/s at 20°C) so

Figure 11. Partial isodelay illustration showing the elevation angles from which initial reflection with a specific time delay can reach a sound source (S) located near the ground. Reflection from the ground is limited to within 10 ms when a sound source is near the ground.

that the difference between the direct and indirect sound paths from S to L can be calculated as:

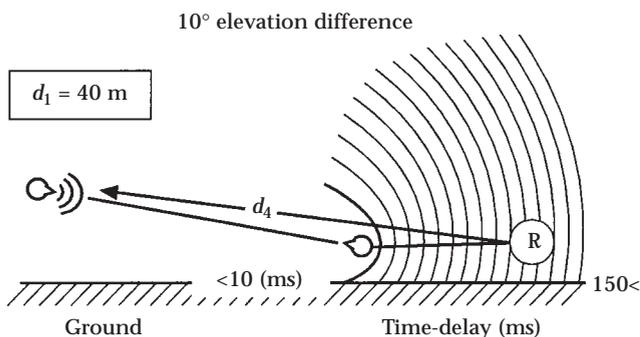$$x = d_2 + d_3 - d_1 = delay * 0.344 \text{ m/ms} \qquad (1)$$

If the listener can associate a conspicuous reflective object R with a discrete reflection using direction, time-delay (augmented by spectrum and amplitude), then it can calculate the direct distance d_1 to the sound source by comparing the delay of reflected sound to that of direct sound (x=delay*0.344 m/ms), the angle between the direct and reflective sound paths (α), and distance to R (d_2):

$$d_1 = \frac{0.5x^2 - xd_2}{d_2(1 - \cos \alpha - x)} \qquad (2)$$

Near-axis reflection

If the sound source S is located somewhere in front and approximately in line with a reflective object R, then (cos α) approaches 1.0 and equations (1) and (2) simplify to:

$$d_1 \simeq d_2 - delay + *0.5*0.344 \text{ m/ms} \qquad (3)$$

In addition to much simpler calculation of source distance, delays of reflected sounds are increased when reflectors are behind the sound source instead of to the side, as shown in Fig. 10. This effect is especially apparent when one compares the spacing of the 10-ms isodelay

ellipses at angles to the side and behind the sound source: the lines are further apart behind than to the side. Thus, reflective objects located behind the sound source will produce more exaggerated echos or reverberation delays than objects to the side. As a result, near-axis reflections might be resolved with greater temporal resolution than those from a discrete off-axis source.

Localization of near-axis reflection may best be described as a relative sound localization task (relative to the direction and distance of direct sound) while localization of off-axis reflection may best be described as an absolute sound localization task (becoming more of an absolute task as time delay and angle of reflection increase relative to direct sound). Relative sound localization tasks are performed with greater accuracy than absolute sound localization tasks (see discussion below, Park 1989 in Klump 1996b). Thus, objects that lie very near to the path of direct sound may be resolved independently of direct sound. In the event that directional cues are not sufficient to distinguish direct sound from reflected sound, amplitude, time delay and frequency spectrum of near-axis reflection may help to distinguish among sound from several possible reflectors.

Elevation

Location and thus distance of a sound source might be inferred by the elevation angle from which direct sound arrives (S–L distance=S–L height difference*cos(S–L elevation angle)). However, for elevation to convey distance, a listener must be perched at an elevation above the sound source and a listener must know the height of the sound source above the ground. Distance estimation will be poor when the elevation angle from which direct sound arrives is small. In this study, initial perches from which birds assessed distance were similar in height to playback speakers and thus elevation of direct sound was probably not being used as a distance cue.

Better performance might be expected when a sound source is near the ground and when a listener is slightly higher than the sound source. Under this condition, useful reverberation (with time delay >10 ms in Fig. 11) is concentrated behind and thus at a higher elevation than direct sound. Early reflections can either be disregarded or suppressed (discussed above). But in either case, reflections arriving from behind and above direct sound may often allow for a relative perception of elevation and a more accurate perception of distance using elevation. We do not know how accurately passerines can resolve the elevation of a sound source. Among birds of prey that hunt by sound, resolution of auditory elevation appears as good as their resolution of auditory azimuth, but raptors that hunt by sight alone do not attend to the elevation of a sound source under test conditions in the laboratory (Rice 1982).

Use of distance cues

We rerecorded towhee calls to maximize the correspondence of acoustic 'degradation' to a specific propagation distance beyond each speaker location at each playback trial site. We tried to capture site-specific cues in our rerecorded stimuli but we did not attempt to recreate the site-specific cues discussed above. Neither direction, amplitude, time delay, nor frequency spectrum of reflected sound in rerecorded signals was useful in tracing discrete reflections back to their original reflectors because these cues were subject to additional reflections from local objects during the final playback.

Accuracy of distance resolution using the cues outlined above is limited by resolution of auditory azimuth, elevation and familiarity with the acoustic environment. Auditory azimuth and path delay are computed automatically from interaural time differences (ITDs) in nucleus laminaris of the avian auditory brain stem (Carr & Konishi 1990). We do not know what degree of knowledge would be required to correlate reflections with objects of known location or by what mechanism that knowledge would be combined with perceived angles and delays to compute auditory distance of the signaller.

Location-specific and signal-specific cues could account for the mixed performance of our birds in the phonotaxis trials with rerecorded stimuli. Birds attending to location-specific cues would fly to a point near the playback speaker (S in Fig. 10), as our birds did in about half the trials, and birds attending to a signal-specific cue (playback SPL) would fly a distance behind the playback speaker determined by rerecording distance and SPL attenuation. Birds scaling both location and signal-specific cues into a combined percept should fly an intermediate distance to rerecorded calls, but the observed bimodal distribution of flight distances is inconsistent with scaling. While indicative of an additional location-specific cue to auditory distance, our data are not sufficient to identify what additional cue is being used. The convincing tests will require experiments designed specifically to tease apart the salient contributions of each cue.

Comparative perception of auditory azimuth

Several laboratory studies have explored the accuracy of auditory azimuth resolution, and our results are strikingly different. With corrections for discontinuity of natural perches, we estimate that towhees can determine auditory distance at about ± 7% of the true auditory distance, and auditory azimuth at about ± 5° of the true auditory azimuth. Without the perch discontinuity correction, ± 8.7° azimuth error could be regarded as our worst-case estimate of the birds' abilities.

Previous studies of auditory azimuth resolution with small birds have used either relative or absolute tests (Klump 1996a). In relative tests of azimuth resolution, the subject must determine whether or when a sound playback is switched from one speaker to another nearby speaker. In absolute tests, the subject must identify the active speaker of two or more. In both test paradigms, the speakers are brought progressively closer together until discrimination falls below some performance criterion, typically 75% correct. Of these two, the absolute test is thought to be the more ecologically relevant (Klump 1996b); however, see our discussion of the near-axis distance cue where relative perception may be more relevant.
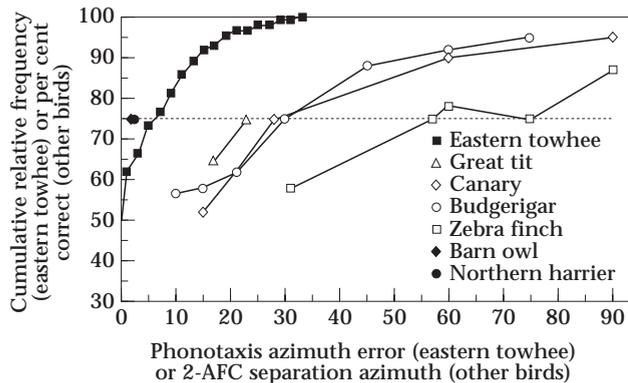
Figure 12. Cumulative relative frequency distribution of azimuths flown in response to playback from a single speaker in this experiment and per cent correct response in 2-AFC tests as distance between perches was changed. Data for canary, budgerigar and zebra finch were in response to conspecific contact calls (Park & Dooling 1991), while data for the great tit, northern harrier (*Circus cyaneus*), and barn owl were in response to wide-band noise stimuli (Knudsen et al. 1979; Rice 1982; Klump et al. 1986).

We can compare the results of our phonotaxis experiment with results obtained in a two-perch forced-choice test (hereafter 2-AFC) by comparing frequency distributions (Fig. 12). Towhee performance ($\pm 5°$) is not as good as owls or harriers (1–2° MRA, Knudsen et al. 1979; Rice 1982), but is better than other birds of similar head size tested in the laboratory with the 2-AFC test (Klump et al. 1986; Park & Dooling 1991). Azimuth resolutions of these birds, estimated from the 75% performance threshold, from best to worst, were 23° MRA (great tit, *Parus major*, wide-band noise), 27° MRA (budgerigar, *Melopsittacus undulatus*, conspecific contact call), 28° MRA (canary, *Serinus canarius*, conspecific contact call), and 57° MRA (zebra finch, *Taeniopygia guttata*, conspecific contact call). Tested for relative sound localization with cardiac-conditioning, minimum resolvable angle for a pigeon, *Columba livia*, was about 6° (Lewald 1987). Pigeons in that study gave extremely variable results and Klump (1996b) argues that the analysis of those data was too liberal in favouring superior performance trials.

Towhee calls are used for both short- and long-distance communication and appear well adapted for localization. Calls consist of a single frequency sweep reaching a peak SPL somewhere between 3 and 4.5 kHz (Fig. 1; B. S. Nelson unpublished data). Calls consisting of a rapid frequency sweep and rapid amplitude decay should be easy to localize (Marler 1955), and small birds tested in the laboratory resolve azimuth most accurately when presented with test signals in the ~4-kHz range (Park & Dooling 1991; Klump 1996a). Thus it appears that the eastern towhee's call may be ideally suited for accurate localization. Even so, call structure alone cannot account for the discrepancy between performance measured in this and other studies of auditory azimuth resolution. Canaries, zebra finches, and budgerigars performed no better on natural vocalizations than they did on noise bursts or on tones presented at their best frequency, even though these natural calls also contain rapid frequency

modulations and energy concentrated at the frequency of best angular resolution (Park & Dooling 1991).

Our birds may have out-performed the birds tested in operant chambers because of the greater distances used in our field trials. At the short presentation distances used in operant chambers, diurnal birds may attend more to visual cues than sound for localization of meaningful objects. Barn owls perform well over such ranges, but they also hunt in darkness and depend on sound to locate prey over short distances (Konishi 1973). If diurnal birds switch their attention from hearing to sight at short distances, operant conditioning may not prove effective in measuring performance of sound localization.

Sound playback in the natural environment produces a sound field with far greater spatial and temporal complexity than occurs in a laboratory test chamber lined with sound-absorbing foam. Not only does sound project in the direct path to the listener, but through reflection and refraction, a sound reaches the listener from many angles with various delays and attenuations. Indirect sound paths have been thought of as extraneous noise that degrades perception of the sound source. We speculate that echo-processing is not always destructive and that reflected sound in a semireverberant open habitat might facilitate azimuth resolution. We suggest, for the sake of argument, that indirect sound paths add redundancy to the direct path cue, and that neural networks for sound localization expect such cues and may even function best in their presence.

Acknowledgments

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