

Vocal tract filtering and sound radiation in a songbird

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Summary

Bird vocalizations resonate as they propagate through a relatively long trachea and radiate out from the oral cavity. Several studies have described the dynamics with which birds actively vary beak gape while singing and it has been hypothesized that birds vary beak gape as a mechanism for varying vocal tract resonances. Nevertheless, few studies have attempted to quantify the effects of beak gape on vocal tract resonances. We replaced eastern towhee, *Pipilo erythrophthalmus* L., syringes with a small speaker and obtained recordings of frequency sweeps while rotating each subject in a horizontal plane aligned with either the maxilla or

mandible. We describe vocal tract resonances as well as how sound radiates as a function of beak gape. Results are inconsistent with the hypothesis that songbirds vary beak gape as a mechanism for ‘tracking’ fundamental frequencies in vocalizations. Instead, decreases in beak gape seem to attenuate resonances that occur between ~4 and 7.5 kHz. We propose that songbirds vary beak gape as a mechanism for excluding and/or concentrating energy within at least two distinct sound frequency channels.

Key words: songbird, vocal production, directional sound radiation, vocal tract resonance, beak gape.

Introduction

Songbirds produce vocalizations using syringeal structures that are located at the caudal end of a trachea that extends several centimeters into the thoracic cavity. Sound resonates when passing through a tube-like trachea and resonance frequencies are determined primarily by tracheal length (e.g. Fletcher and Tarnopolsky, 1999). Since birds often produce a wide range of sound frequencies in their vocalizations, it has been suggested that birds vary beak gape as a mechanism for altering the effective length of the vocal tract (e.g. Fletcher and Tarnopolsky, 1999; Nowicki and Marler, 1988). In addition, it has been hypothesized that relatively small birds vary beak gape as a mechanism for ‘tracking’ or emphasizing fundamental frequencies (f_0) in vocalizations relative to higher harmonics (Fig. 1A; e.g. Hoese et al., 2000; Nowicki and Marler, 1988; Podos et al., 2004; Westneat et al., 1993).

In contrast with these theoretical predictions, experimental results reported for the European blackbird (*Turdus merula*) suggested that changes in beak gape might simply alter the amplitudes of sound frequencies above ~4 kHz (Fig. 1; Larsen and Dabelsteen, 1990). These authors do not describe vocal tract resonances. Nevertheless, several subsequent studies have reported results in which it remains unclear whether birds vary beak gape as a mechanism for ‘tracking’ fundamental frequency or as a mechanism for controlling amplitude above ~3–4 kHz (Fig. 1B; e.g. Goller et al., 2004; Nowicki, 1987;

Podos et al., 2004; Suthers and Goller, 1997; Westneat et al., 1993).

To distinguish between these two alternatives we replaced eastern towhee, *Pipilo erythrophthalmus* L., syringes with a small speaker and quantified how sound radiates as a function of: (1) sound frequency, (2) head and body orientation and (3) beak gape. We propose that small birds do not vary beak gape as a mechanism for ‘tracking’ fundamental frequencies in vocalizations, but instead decrease beak gape as a mechanism for controlling the amplitudes of sound frequencies between approximately 4 and 7.5 kHz.

Materials and methods

Four male eastern towhee subjects (358, 390, 430 and BB) were captured as juveniles near Bloomington, Indiana, USA, and held in captivity for at least 2 years. Subjects were overdosed with isoflurane (Halocarbon Laboratories, North Augusta, South Carolina, USA) and the lower third (approximately 1 cm) of each bird’s trachea was separated from connective tissue and separated from the top quarter of the syringeal muscle just below the last free cartilaginous tracheal ring. A 3 mm length of Teflon heat shrink tube (1.14 mm max. diameter, 0.2 mm wall; Small Parts; Miami Lakes, Florida, USA) was then attached to the port of a small speaker (EP-7108; Knowles, Itasca, Illinois, USA) and the

shrunk end (0.99 mm min. diameter) of the tube was inserted into the end of the trachea so that the base of the speaker port was located where the labia normally vibrate (Fig. 2).

Subjects were next mounted above the top of a 60 cm (0.96 cm diameter) steel pole in a natural posture by clamping the upper half of each leg between two small sheets of perforated aluminum (3–6 cm×2.5 cm×0.8 mm, 127 1.1 mm diameter holes per cm²; Small Parts). Each subject's head was then positioned as described below using a rigid steel wire (~50×1.2 mm diameter) glued to the mandible and to the top of the 60 cm pole. Mounted subjects were next positioned at least 60 cm from each wall of a humidified 2.0×2.4×2.75 m sound-attenuating chamber (Industrial Acoustics Company, Inc., Bronx, New York, USA) that was lined with at least one layer of acoustic foam (classic 7.62 cm wedges; Sonex, Minneapolis, Minnesota, USA) to absorb reflections that might otherwise occur from the semi-reflective perforated steel walls of the chamber.

We generated and played frequency sweeps from the speaker, as opposed to noise or recorded vocalizations, to maximize signal to background noise ratios and to simplify spectral comparisons. Linear frequency sweeps (1 s, 0.5–11.0 kHz) were generated with 10 ms raised cosine onset and offset ramps using an array processor [AP2; Tucker–Davis Technologies (TDT), Alachua, Florida, USA]. Sweeps were then played from the speaker using a digital to analog converter (DD1; TDT; 16 bit, 40 kHz) and attenuator (PA4; TDT; –52 dB). Sweeps were recorded using a 1/2 inch microphone (4189; Brüel & Kjaer, Nærum, Denmark) mounted on the end of a threaded rod (90×0.95 cm) and positioned 90 cm from the opening of each subject's glottis (2671 preamplifier, WB 1372 power supply; Brüel & Kjaer; MP-1 preamplifier; Sound Devices, Reedsburg, Wisconsin, USA; 160 Hz –6 dB octave⁻¹ high-pass filter with no gain; ULN-2 preamplifier; Metric Halo, Hopewell Junction, New York, USA; 66 dB gain). Recordings were digitized (DD1; TDT; 16 bits, 40 kHz, 15 kHz anti-alias filter) and saved to disk using an array processor (AP2; TDT). Spectra were generated using 1000 point (40 ms) Hanning windows that were overlapped (98%) and averaged over the duration of each stimulus (Igor Pro v4; Wavemetrics, Lake Oswego, Oregon, USA).

Sound radiation

To quantify how sound radiates as a function of beak gape we varied head and body orientation in 9° increments over 360° around a single vertical axis leading from the top of the pole on which subjects were mounted to the opening of the glottis. Orientation was controlled using a stepper motor (5×5×5 cm) mounted 60 cm below the subject's abdomen and on the top of a tripod that was positioned near the floor and covered with acoustic foam (7.62 cm wedges). Recordings were also obtained from two subjects (390 and 430) with three beak gapes (2, 6 and 11 mm) after the microphone was positioned at either a higher (+20°) or lower elevation (–20°) relative to where the microphone was normally positioned (see below).

Beak gape

Frames (3–11×40 mm) made from of steel wire (1 mm diameter) were used to vary beak gape (i.e., the distance between the tips of the maxilla and mandible; Fig. 2). A small amount of heated glue was used to prevent the wire frame from moving as subjects were rotated. Unless otherwise noted, the mandible was directed towards the microphone and we varied only the vertical angle of the maxilla (and head). One subject (430) had grown a small 'hook' on the tip of his maxilla and in this case the upper wire was placed just behind the hook and measurements were obtained relative to the lower edge of the maxilla immediately behind the hook. Measurements of beak gape were accurate to within no more than ±0.2 mm although individual differences in beak size and shape preclude precise comparisons between individuals.

To test whether results might differ when the maxilla is held in place, and when the position of the mandible is varied, we replicated measurements obtained for subject BB after gluing the maxilla to the top inside edge of a steel wire loop (1×30 mm). We then varied only the orientation of the mandible while the orientation of the maxilla was held constant and directed towards the microphone.

Resonances

We estimated tracheal resonances by comparing recordings described above with reference recordings that we obtained after mounting the speaker alone, without the bird, above an identical 60 cm (0.96 cm diameter) steel pole using a small amount of glue and a 2 cm steel wire (1 mm diameter). No tubes were attached to the speaker and the speaker was positioned by itself close to where the glottis was positioned in each mounted subject (90 cm or 15 cm from the microphone). Reference spectra were obtained with the speaker port directed towards the microphone, however spectra varied little as the speaker was rotated (s.d.<2 dB, 1–10 kHz, 0–360°).

We also obtained recordings at a distance of 15 cm from the glottis after laying each subject on a horizontal platform made from perforated aluminum (127 1.1 mm diameter holes per cm²). Recordings were obtained while gently stretching or shortening the trachea relative to what was deemed to be each trachea's natural length (i.e., the *in vivo* distance from the syrinx to where connective tissue was removed). Recordings were obtained from two subjects after removing either a 5 mm (subjects 430 and BB) or 8 mm (subject 430) segment from the trachea and re-inserting the speaker into the shortened trachea.

Controls

Recordings were terminated after 4–5 h and initial recordings were repeated to ensure that no acoustical changes occurred within the vocal tract during this period. In addition, recordings were obtained using a random assortment of beak gapes (subject 358) or were obtained for odd valued beak gapes (11 mm, 9 mm, etc.) before even valued beak gapes (10 mm, 8 mm, etc., subjects 390, 430 and BB). Visual inspection of the glottis indicated that no obvious physical changes occurred

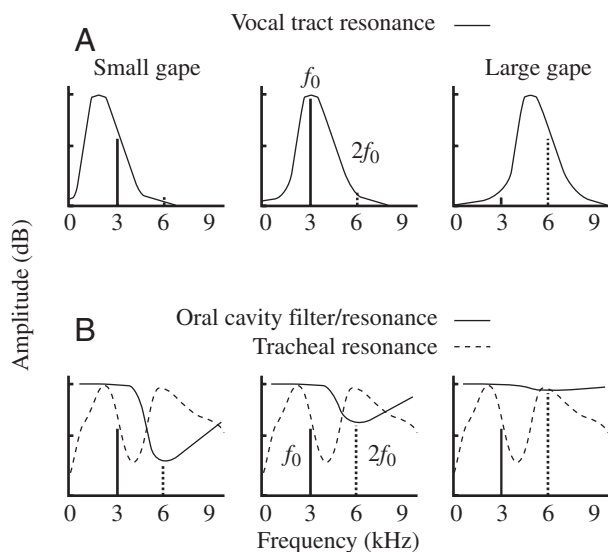


Fig. 1. (A) Illustration of how a variable frequency resonance filter might 'track' fundamental frequency (solid vertical lines) as beak gape increases (as conceived by Hoese et al., 2000). (B) Illustration of how a filter with a single cut-off frequency near 4 kHz that is controlled by beak gape (solid lines) might function to attenuate tracheal resonances (broken lines) that occur above ~ 4 kHz. Beak gape increases from the left graph to the right graph.

during the recording period. The exposed lower portion of the trachea dried slightly but could still be stretched and longitudinally compressed at the end of the experiment.

To ensure that spectra generated from frequency sweeps were not biased, we occasionally recorded noise signals (WB 1314 noise generator; Brüel & Kjaer; 10 s, 0.4–11 kHz, 45 dB attenuation). In all cases, spectra obtained from frequency sweeps were similar to those obtained from smoothed recordings of noise signals (± 1 dB).

To ensure that recordings were not biased due to microphone or subject locations within the acoustic chamber we obtained recordings at a distance of 90 cm from several wooden spheres (3.0, 2.5, 2.0 and 1.8 cm diameter) after inserting a silastic tube (4.5 cm long, 1.47 mm i.d., 1.96 mm o.d.) through the middle of each sphere. Spectra obtained as spheres were rotated (360°) did not vary when spheres were positioned in different locations within the chamber (± 1 dB). Spectra for some orientations varied when spheres were placed next to a wall (within 20 cm, ± 2 dB), however subjects and microphones were always positioned at least 60 cm from each wall.

Although the interface between the Teflon tube, speaker port and trachea was secured with a suture and a small amount of adhesive glue during each experiment, some sound may have radiated from this junction or from the exposed portion of the trachea. To assure that sound from these sources did not influence our recordings we obtained additional recordings after inserting a silastic plug (2 \times 8 mm) into the glottis and clamping the beak in a closed position (0 mm, Fig. 3). We do not know how effective this plug was in attenuating sound, or if it caused sound to radiate from other locations (e.g. from the

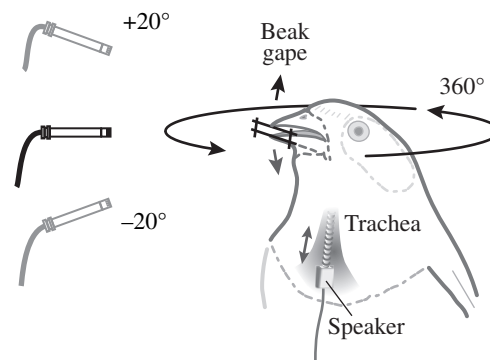


Fig. 2. Illustration showing where a small speaker was inserted into the trachea, how beak gape was varied, and how subjects were rotated with respect to microphone positions. Beak gape was measured as the distance between the tips of maxilla and mandible.

larynx or upper portion of the trachea). As a conservative precaution we excluded frequency bins in spectra above 10 kHz that sometimes fell below threshold levels that were obtained under these conditions. Substantial low frequency noise existed in the chamber and this required us also to exclude sound frequencies below 1 kHz.

Harmonic amplitude and beak movements

Our results suggest that towhees may sometimes vary beak gape as a mechanism for attenuating harmonics (see Discussion). We therefore measured the amplitudes of second harmonics ($2f_0$) from 1067 'tow-hee' calls that were recorded from 36 Florida towhees that were held in a small cage (20 \times 20 \times 20 cm, 1.15 \times 2.25 cm mesh, 2.4 mm diameter wire; see Nelson 2000, 2004 for further details). Recordings were obtained using one or two measuring microphones placed 100 cm from the center of the cage (4188 microphone with 2671 preamplifier; Brüel & Kjaer; see Nelson, 2002, 2004 for further details).

Fundamental frequency was estimated using an autocorrelation algorithm (1.5 ms window), however harmonic amplitudes were measured from spectra that were extracted from time-frequency spectrograms (44.1 or 48 kHz sampling rate, 34.8 ms Hanning window, 46.4 ms FFT frame, and 98% overlap between each successive 46.4 ms frame, $6.97e-4$ s frame rate; see Nelson 2004 for further details). Absolute amplitudes were calculated using 94 dB (relative 20 μ Pa) calibration signals (see Nelson, 2000). For clarity, however the amplitudes of second and third harmonics were scaled relative to the amplitudes of fundamental frequencies. Means and standard deviations were calculated for harmonics corresponding with fundamental frequencies that fell within 100 Hz bins.

We do not attempt to provide a thorough description of how towhees vary beak gape while vocalizing. As support for our hypotheses, however we analyzed video recordings that were obtained previously of seven male Florida eastern towhees and six male Indiana eastern towhees (Nelson, 2000; B.S.N., unpublished). Three of the Florida birds were video taped from

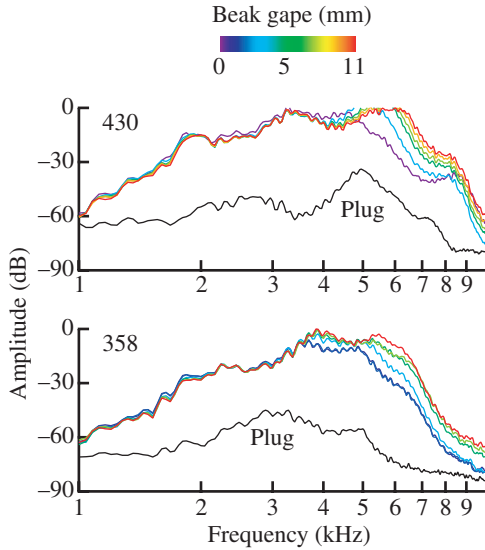


Fig. 3. Representative spectra of frequency sweeps recorded from two subjects (colored lines, 358 and 430) and spectra obtained after placing a silastic plug into the glottis and closing the beak (0 mm, black lines). Spectra are referenced to peak amplitude (1–10 kHz). Spectra obtained for subjects 390 and BB under these same conditions are similar (see Figs 4–7).

a distance of 2–3 m while they were held in a small cage (see above) using a Hi-8 video camera (ES6000; Canon, USA). Analog recordings were then transferred to a digital video camera (TRV-900; Sony, USA) and then to a computer for analysis (CatDV v3; Square Box Systems, Stratford-upon-Avon, UK; sampling rate = 30 frames s^{-1}). Four free-ranging Florida towhees were video taped outside of the cage from a distance of 4–5 m (ES6000; Canon or TRV-900; Sony). All six Indiana birds were video taped from a distance of 2–3 m (TRV-900; Sony) while they were held in the cage. Recordings obtained with the digital video camera were transferred directly to a computer.

Beak gape was measured from video frames using custom computer procedures (Igor Pro v4) and was defined as the distance between the tips of the maxilla and mandible. Raw measurements of beak gape were obtained by placing cursors on these tips and by calculating the linear distance between the cursors (within each 720×480 point video frame). Raw measurements were then converted into measurements of beak gape (mm) using a reference defined as the distance from the anterior end of the nares to the tip of the maxilla (Podos et al., 2004). The conversion was made using a scaling factor that was calculated as the ratio between the raw distance from the anterior end of the nares to the tip of the maxilla (within the 720×480 point video frame matrix) and the same distance that was measured using calipers from real birds (see below). When possible, scaling factors (1.7–2.3) were obtained during vocalizations but were often obtained from previous or subsequent frames. Reference distances were always obtained when the head was perpendicular to the camera. Reference distances could not be obtained from video taped subjects. As

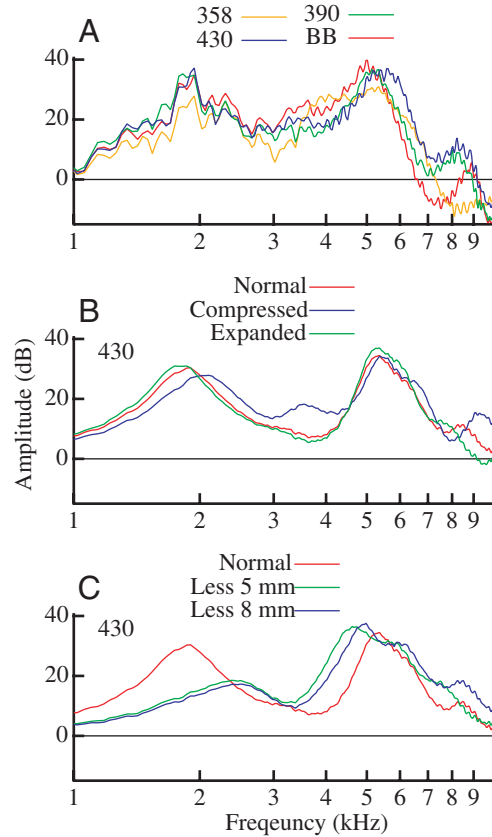


Fig. 4. Vocal tract resonances emphasize sound frequencies near ~2 and 5.5 kHz. (A) Vocal tract resonances estimated as the difference between a spectrum obtained from the speaker mounted by itself (black line at zero) and spectra recorded after inserting the port of the speaker into the trachea, setting beak gape at 5 mm, and orienting each subject towards the microphone (0° , colored lines). (B) Vocal tract resonances estimated from recordings obtained at a distance of 15 cm from horizontally oriented subjects. The normal condition represents a trachea length that was deemed as natural. The trachea was then shortened or lengthened by gently pushing or pulling on the cut end of the trachea. (C) Vocal tract resonances estimated as in B after removing 5 mm or 8 mm segments from the exposed portion of the trachea. Results for subjects 390 and BB are similar. Spectra in (A) are noisy (rippled) because these recordings were obtained at a distance of 90 cm. Spectra in (B) and (C) are less noisy because these recordings were obtained at a distance of 15 cm.

a consequence, we used mean values calculated from birds within each population (reference distance = 10.5 ± 0.1 mean \pm s.d., $N=3$ for FL subjects, 9.8 ± 0.1 , $N=15$ for IN subjects). Overall measurement accuracy depended on the quality of our recordings but is not believed to have exceeded ± 1.5 mm.

Many factors limited the number of measurements that could be obtained (Florida: 362 frames from 50 calls, $N=18$, 6, 6 calls in the cage; 9, 6, 4, 1 calls outside of the cage; Indiana: 854 frames from 97 calls, $N=53$, 15, 13, 10, 5, 1). For example, in addition to limitations described by Podos et al. (2004), we could not obtain measurements when the tips of the beak were hidden by the cage. To ensure that intermediate beak gapes and midrange sound frequencies were not under-sampled we

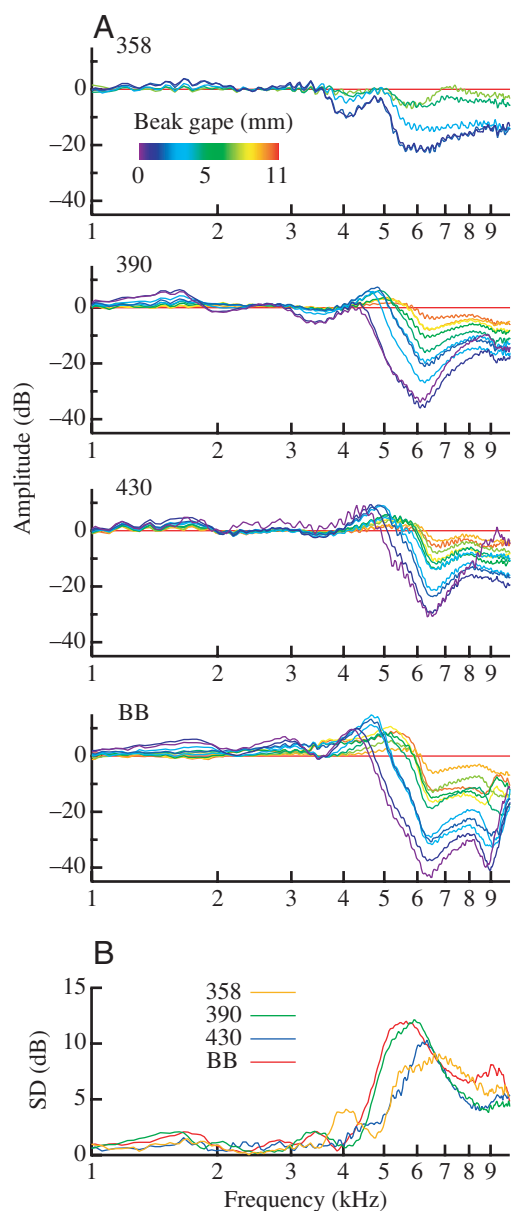


Fig. 5. Vocal tract resonances do not vary with beak gape below ~ 4 kHz. Instead decreases in beak gape attenuate sound frequencies between ~ 4 and 7.5 kHz. (A) Spectra obtained for different beak gapes plotted relative to a spectrum obtained with a maximum beak gape (11 mm). (B) Standard deviations (s.d.) calculated across spectra displayed in A.

excluded calls in which we could not obtain three consecutive measurements. In addition, we excluded calls if these three consecutive measurements did not encompass the loudest part of each call.

Measurements of peak frequency that are presented together with measurements of beak gape were obtained from 3.33 ms audio segments (sampling rate = 48 kHz), corresponding with extracted video frames. Measurements of peak frequency within each 3.33 ms audio segment were calculated using a previously described autocorrelation algorithm (Nelson, 2004; measurements correspond well with measurements obtained

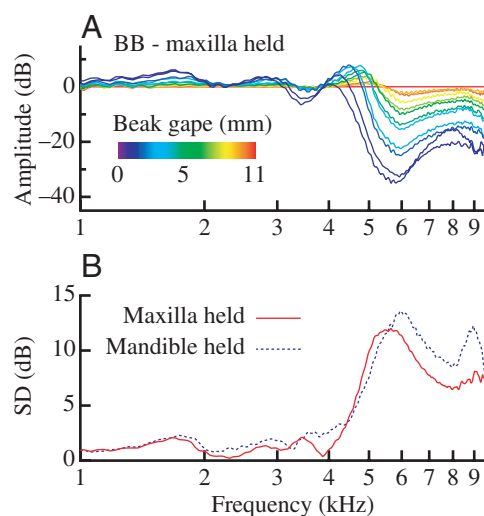


Fig. 6. Vocal tract resonances do not vary below ~ 5 kHz regardless of whether the orientation of the maxilla or mandible is held constant (see Fig. 5A for comparison). Spectra obtained under these two conditions vary above ~ 5 kHz, however these differences can likely be attributed to differences in head diameter or differences in vertical head orientation. (A) Spectra obtained for different beak gapes plotted relative to a spectrum obtained with a maximum beak gape (11 mm). (B) Standard deviations (s.d.) calculated across spectra displayed in A.

from spectra, 1600 point FFT). Audio recordings were obtained using each video camera's built-in microphone. Measurements obtained from these recordings did not vary when compared with recordings obtained simultaneously from a distance of 100 cm (see above).

Results

Vocal tract resonances

Inserting the speaker so that it is flush with the outside edge of an acoustic baffle (e.g. a wooden sphere with a diameter that approaches sound wavelength) increases acoustic output in the forward direction. Resonances within the vocal tract seem to further amplify sound frequencies near approximately 2 and 5.5 kHz, relative to amplitude levels measured from the sound source (speaker) alone or when the sound source was inserted into a baffle, but not over intermediate sound frequencies (Fig. 4A). Throughout this paper we use the terms 'amplification' and 'emphasis' to refer to increased sound level at the position of the microphone under certain experimental conditions, not as gain applied to the source.

Towhee tracheas are ~ 45 mm long and ~ 1 mm in diameter. Resonances observed correspond well with odd numbered quarter wavelength resonances near 2 and 5.5 kHz that are predicted for a stopped tube of this length near 1.88 kHz and 5.67 kHz (Fig. 4). Resonance frequencies remained relatively constant even as the trachea was stretched or compressed so as to slightly increase or decrease the distance between exposed cartilaginous rings (Fig. 4B). Resonances changed slightly when the trachea was shortened 5 or 8 mm. In particular, the

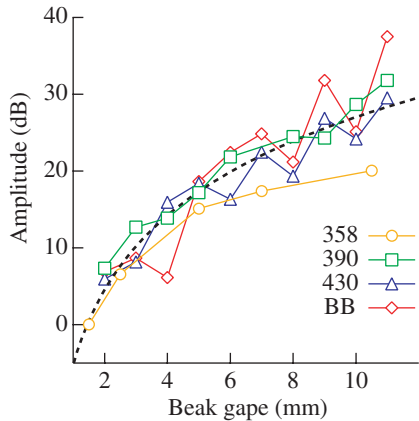


Fig. 7. We observed substantial changes in amplitude at 6.5 kHz as beak gape was varied between 0 and 11 mm. Amplitude increases linearly with beak gape at 6.5 kHz but is plotted on a logarithmic scale (dB). Amplitude at this frequency across all subjects can be approximated as $A = -5 + 32 \log(B)$, where A is amplitude (dB) and B is beak gape (broken line). Amplitude values are plotted relative to those obtained with a closed beak (0 mm).

resonance peak that we observed near 2 kHz when the trachea was at a normal length both decreased in magnitude and was shifted to a slightly higher frequency under these experimental conditions (Fig. 4C).

Beak gape

Changes in beak gape did not substantially shift the resonance frequency of the vocal tract. Instead, changes in beak gape seem to amplify or attenuate sound frequencies between ~4 and 7.5 kHz depending on which beak gape is chosen as a reference (Fig. 5A). To assess the frequencies over which changes in beak gape had the greatest effect we calculated standard deviation (S.D.) across spectra that are plotted in Fig. 5A (Fig. 5B). Calculations of S.D. are minimally dependent on which beak gape is chosen as a reference and again suggest that changes in amplitude will occur between ~4 and 7.5 kHz with smaller changes in amplitude occurring between ~7.5 and 10 kHz.

Decreases in beak gape sometimes amplified sound frequencies between ~3.5 and 5.5 kHz at the position of the microphone (subjects 430 and BB). This increase in amplitude should be viewed with caution, however, since the relative differences that are evident in Fig. 5A are dependent on the 11 mm gape reference spectrum that was used to derive each additional spectrum. Indeed, these relative differences vary by a small amount when we choose a different reference beak gape. Nevertheless, relative differences between ~3.5 and 5.5 kHz that are evident in spectra shown in Fig. 5A are also evident in raw spectra (see Fig. 3). As a consequence, it remains possible that a decrease in beak gape might sometimes amplify sound frequencies between ~3.5 and 5.5 kHz (primarily near ~4 kHz).

Spectral peaks shift in frequency between ~4 and 5.5 kHz as beak gape varies (Fig. 5A). Again, however these relative differences change when we choose a different reference beak gape. In addition, shifts in these spectral peaks may occur, in part, due to small changes in head diameter or vertical changes in head orientation that occurred as beak gape was varied. Thus, shifts in spectral peaks that are evident between ~4 and 5.5 kHz in Figs 5 and 6 should be viewed with caution.

Increasing beak gape by repositioning the mandible, as opposed to the maxilla, did not substantially alter results below ~5 kHz (Fig. 6). Sound levels increased above ~5 kHz when the upper mandible was held in a constant position, although much of this increase can be attributed to differences in head diameter or differences in vertical head orientation and not beak gape.

Amplitude levels varied considerably with beak gape near 6.5 kHz in all subjects and amplitude, at the position of the microphone, increased linearly with beak gape at this frequency (Fig. 7). These results suggest that relatively small changes in beak gape will result in relatively large changes in amplitude above ~4 kHz as long as birds do not open their beaks beyond ~5 mm (when amplitude is viewed on a logarithmic scale, dB). Conversely, sound frequencies above ~4 kHz will attenuate the least when birds increase beak gape beyond ~5 mm. It should be noted, however that increases in amplitude that occur with beak gapes larger than 5 mm may, in some cases, be lost if subjects are not oriented towards a receiver (or have their heads directed upwards) since vocalizations also become more directional as beak gape increases (see below).

Sound radiation

Sound radiation patterns were relatively simple and, in all cases, consisted of a single amplitude decrement near $\pm 130^\circ$ (Fig. 8). The width (in degrees) of this amplitude decrement increased with sound frequency and seems to explain decreases in amplitude that were observed across all directions.

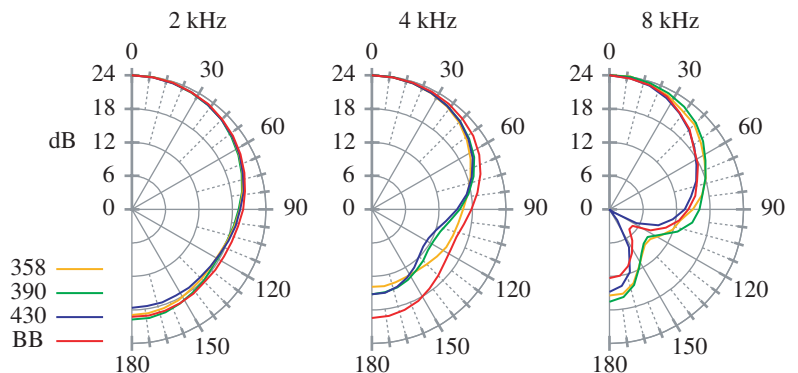


Fig. 8. Sound radiates from subjects in a relatively simple manner and a single amplitude decrement of variable width (degrees) and depth (dB) near $\sim 130^\circ$ explains most changes. Plotted are amplitudes at 2, 4 and 8 kHz extracted from spectra of recordings obtained from subjects with a 5 mm beak gape. Measurements are averaged across each hemifield ($0-171^\circ$) and are normalized relative to 0° .

Differences in radiation patterns are difficult to summarize both as a function of beak gape and sound frequency. As a consequence, we summarize how sound radiates as a function of these two factors using calculations of s.d. (calculated across 360°, $N=40$, 9° increments). s.d. increased positively with sound frequency and beak gape, although relatively large increases in s.d. occurred between ~3 and 3.5 kHz and again near ~7 kHz (Fig. 9). s.d. calculations increased over relatively high sound frequencies after we lowered the elevation of the microphone (-20°) but decreased after we increased the elevation of the microphone ($+20^\circ$; Fig. 10).

Individual differences

The shapes of the filter functions that we observed above ~4 kHz varied between subjects (Fig. 5). We do not know if these differences represent physical differences that exist in living subjects or whether these differences might simply represent differences in how subjects were prepared and mounted before recordings were obtained. In either case, however, the differences that we observed might represent variation that occurs naturally as subjects change the configuration of their vocal tract or overall posture. Some of the differences that are evident in Figs 5 and 6 can also be attributed to individual differences in reference spectra (i.e., spectra obtained with ~11 mm beak gapes).

Calculations of directivity (s.d.) exceeded ~3 dB near 3.5 kHz in subjects 358 and BB but exceeded ~3 dB near 3 kHz in subjects 390 and 430 (Fig. 9). These differences may again correspond with differences in how subjects were prepared and mounted before recordings were obtained. Nevertheless, these differences might also be explained by differences in body size since directionality is presumed to depend, in part, on body size. Subjects 358 and BB, for example, weighed only 34 and 36 g while subjects 390 and 430 weighed 56 and 54 g. Our sample size does not allow us to establish a clear relationship between directionality and body weight. Nevertheless, our results are consistent with the hypothesis that sound radiates from larger subjects in a more directional manner. Wild-caught towhees in Indiana weigh 39–50 g (43.5 ± 2.7 g, mean \pm s.d., $N=20$) and thus our results are likely to span differences in directionality that might occur within this population due to typical differences in body size.

Harmonic amplitude and beak movements

Second harmonics in Florida ‘tow-hee’ calls, on average, have relatively low amplitudes between ~4 and 8 kHz (<-30 dB; Fig. 11A). Harmonic amplitudes are highly variable although much of this variation can likely be attributed to variation in subject orientation (Fig. 9).

Towhees in both Indiana and Florida tend to produce low sound frequencies (<-3.5 –4 kHz) with small beak gapes (<-4 mm), but produce higher sound frequencies with large gapes (>4 mm) or a wide range of beak gapes (0–10 mm; Figs 11B and 12). In most cases, subjects produced high frequencies (>-4 kHz) with a small beak gape (<-4 mm) as calls were ending. Relatively few measurements were obtained

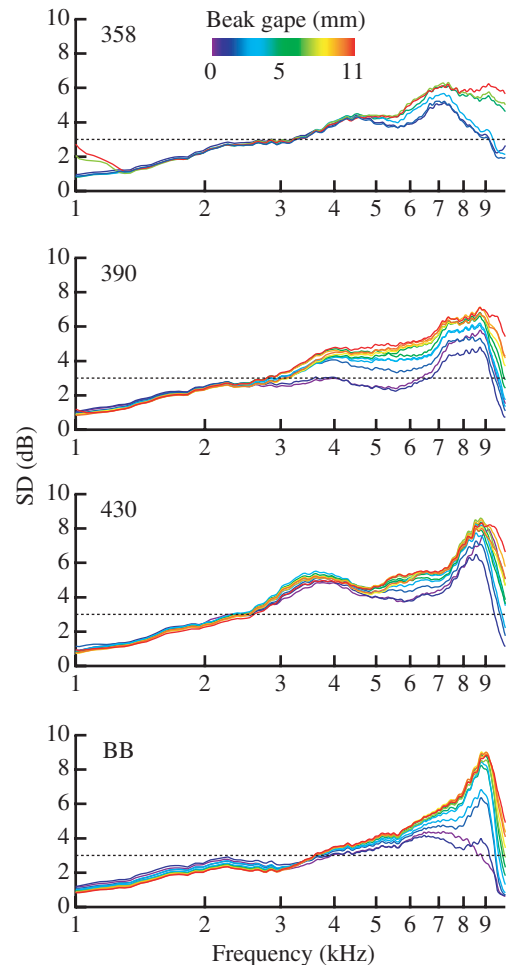


Fig. 9. Acoustic output becomes more directional as sound frequency increases and as beak gape increases. Directionality calculated as s.d. across 360° ($N=40$) is plotted independently for each beak gape (colored lines) and as a function of sound frequency. Broken lines at 3 dB are included as references (see text).

for intermediate beak gapes (~4 mm) and midrange sound frequencies (~3.5–4.0 kHz) even though calls were not analyzed if beak gapes corresponding with these midrange frequencies could not be measured.

Subjects often increased beak gape (to ~0.5–2.0 mm) shortly before (1–2 frames) producing the relatively loud sinusoidal frequency ‘sweep’ that characterizes this call. This increase in beak gape corresponds with a low-level, rapidly modulated, sound that is often emitted prior to call onset (within ~25 ms, not illustrated). In addition, one subject tended to maintain a relatively large beak gape (~5 mm) throughout the recording period. Nevertheless, all subjects began producing the ‘sweep’ with a small beak gape (<-1 mm) even if this required a brief (1–2 frames), presumably rapid, decrease in beak gape (not illustrated). ‘Tow-hee’ calls are highly variable in acoustic structure (Nelson, 2000) and it should be noted that low frequency Indiana calls (<-3 kHz) and high frequency (>-4 kHz) Florida calls may be underrepresented in our sample.

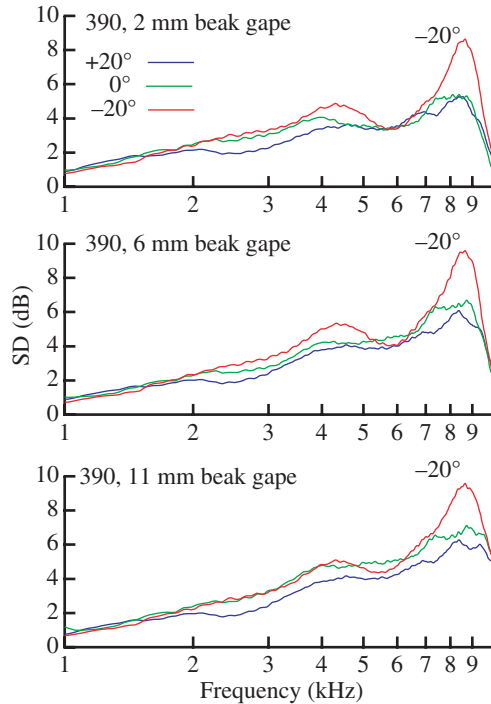


Fig. 10. Acoustic output became more directional when the microphone was lowered 20° but became less directional when the microphone was elevated 20°. Directionality (s.d.) was calculated as in Fig. 9.

Discussion

Our results do not support the hypothesis that songbirds vary beak gap as a mechanism for ‘tracking’ fundamental frequencies in vocalizations. Instead, our results suggest that towhees vary beak gap as a mechanism for controlling the amplitudes of sound frequencies between ~4 and 7.5 kHz. Results also suggest that vocalizations become more directional as beak gap increases and that vocal tract resonances, in general, function to emphasize sound frequencies below ~3 kHz and above ~4 kHz.

Vocal tract resonances

Audibility functions obtained for numerous avian species demonstrate that birds are most sensitive to sound frequencies near 3 kHz (Dooling et al., 2000). Many songbirds and non-passerines alike often produce strong frequency components in vocalizations near 3 kHz and may do so in order to increase efficacy of communication over distance (e.g. Wiley and Richards, 1978; Wright et al., 2003). Our results suggest that tracheal resonances, and perhaps vocal tract resonances as a whole, function to emphasize sound frequencies near 2 and 5.5 kHz as opposed to near ~3 kHz. Thus, vocal tract resonances might function to increase the distance over which modulated vocalizations spanning ~1.5 to 7.5 kHz can be used as effective communication signals. Towhees and other songbirds, for example, often modulate their vocalizations over a relatively wide range of sound frequencies (see below, Wiley and Richards, 1982) and vocal tract resonances (near 2 and

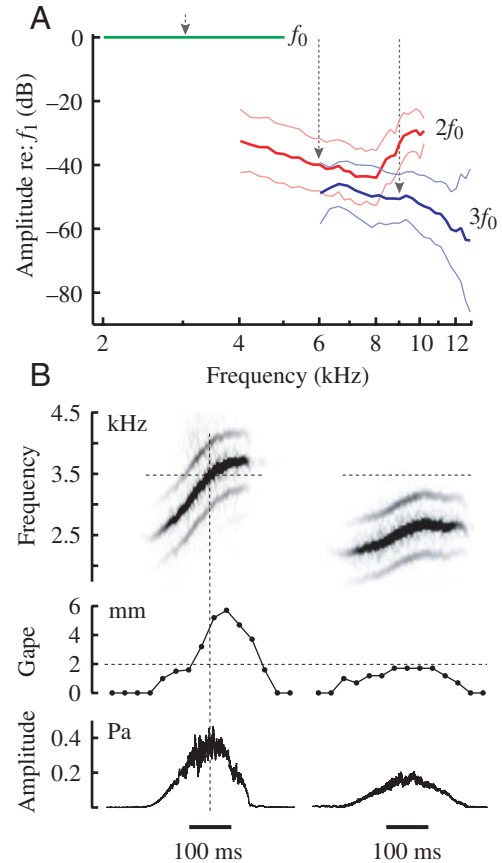


Fig. 11. (A) Second harmonics ($2f_0$) in Florida ‘tow-hee’ calls have relatively low amplitudes. These results suggest that harmonics with frequencies above ~4 kHz may be strongly attenuated. Illustrated are the mean relative amplitudes (thick lines) of harmonics in calls produced by 36 Florida subjects ($N=1067$). Thin lines represent the addition or subtraction of one standard deviation. (B) Representative time-frequency spectrograms of two Florida tow-hee calls, measurements of beak gape obtained from video recordings, and amplitude traces for each call.

5.5 kHz) may function to increase the distance over which these modulated vocalizations can be detected and discriminated (Lohr et al., 2003).

The towhee’s trachea is ~45 mm long and odd numbered, quarter length, resonances predicted near 1.88 kHz and 5.67 kHz correspond well with resonances in our recordings. It remains possible that songbirds are able to alter these resonances by changing the configuration of the larynx. Alternatively, tracheal resonances may remain relatively stable (Daley and Goller, 2004).

Beak gape

Our results suggest that sound frequencies between ~4 and 7.5 kHz will be attenuated whenever towhees reduce the gape of their beak. This result is inconsistent with the hypothesis that variation in beak gape functions to shift the resonance frequency of the vocal tract since resonances that can be attributed to the trachea did not shift upwards or downwards

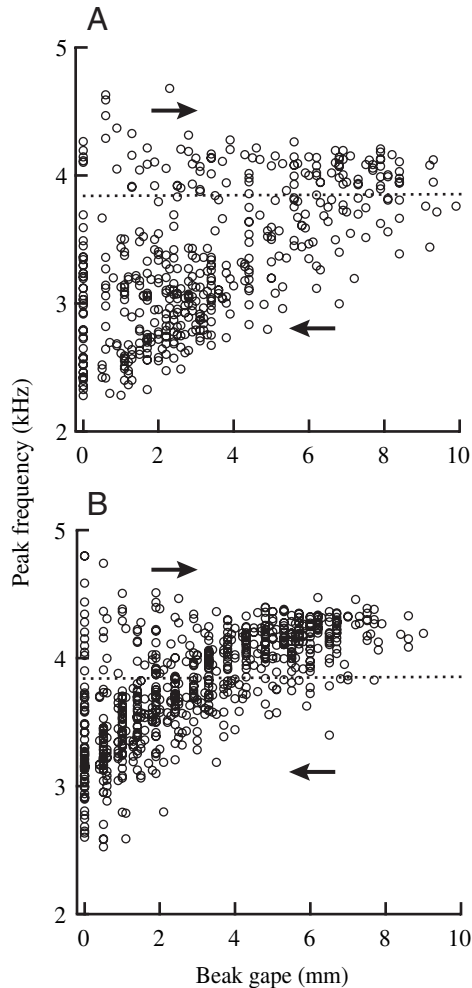


Fig. 12. Towhees tend to produce low sound frequencies in 'tow-hee' calls with a small beak gape but produce high sound frequencies with a large beak gape. Plotted are measurements of beak gape and measurements of peak sound frequency obtained from audio frames corresponding with video frames. (A) Calls recorded in Florida (362 frames from 50 calls produced by seven subjects). (B) Calls recorded in Indiana (854 frames from 97 calls produced by 6 subjects). Sound frequencies above the dashed line (~ 3.75 kHz) seem to be attenuated as towhees close their beaks (Fig. 5). Arrows depict directional pressures that are described in the text.

in frequency as we varied beak gape. In particular, we did not observe shifts in resonance frequency that were predicted to occur over relatively low sound frequencies ($< \sim 3.5$ kHz, e.g. Hoese et al., 2000; Podos et al., 2004). Nevertheless, our data are consistent with spectral changes that were observed in the European blackbird (Larsen and Dabelsteen, 1990) and with results that have been reported for living subjects. For example, spectral changes in the songs of several species that were reported by Nowicki (1987) and Hoese et al. (2000) appear to occur primarily above ~ 3.5 kHz. Similarly, spectral changes reported by Goller et al. (2004) in zebra finches, *Taeniopygia guttata*, occur primarily over relatively high sound frequencies. Suthers and Goller (1997) also demonstrated that harmonics of fundamentals below ~ 3.5 kHz tend to be suppressed when

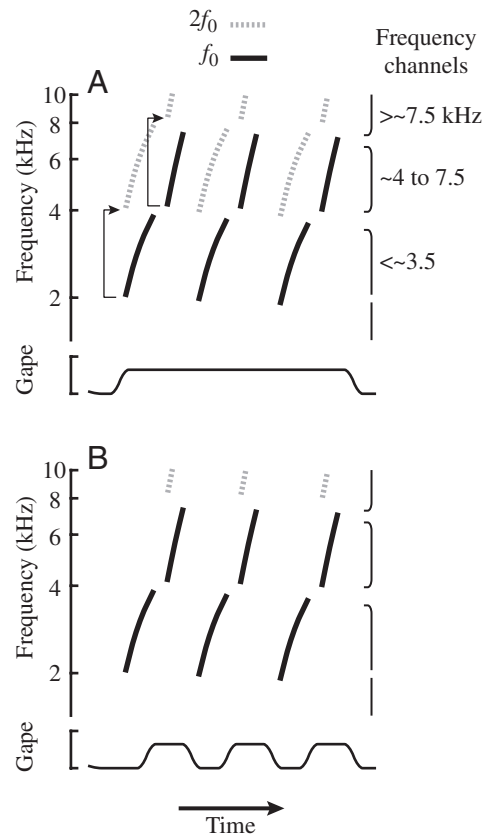


Fig. 13. Schematic time-frequency spectrogram illustrating how the harmonics of notes in vocalizations with frequencies between ~ 4 and 8 kHz (i.e., harmonics of fundamental frequencies between ~ 2 and 4) might degrade temporal patterns across preceding or subsequent notes when these preceding or subsequent notes are produced with fundamental frequencies between ~ 4 and 8 kHz. (A) Illustration where second harmonics are 'weakly attenuated' between ~ 4 and 8 kHz. Arrows point to where harmonics occur and how the frequencies of these harmonics correspond with hypothetical sound frequency channels defined on the left side of the figure. (B) Illustration where second harmonics are 'strongly attenuated' between ~ 4 and 7.5 kHz.

northern cardinals, *Cardinalis cardinalis*, sing songs with relatively small beak gapes.

Podos et al. (2004) used linear regression to describe correlations between fundamental frequency and beak gape movements in several of Darwin's finches under the assumption that monotonic (or linear) changes in beak gape might be used to 'track' fundamental frequency (Fig. 1A). Nevertheless, many of these species appear to use either a relatively small beak gape ($< \sim 5$ mm) when producing relatively low fundamental frequencies ($< \sim 3.5$ kHz) or employ a relative large beak gape ($> \sim 5$ mm) when producing high fundamental frequencies ($> \sim 3.5$ kHz; Podos et al., 2004). As a consequence, intermediate gapes might occur during transitions between these two ends and birds may simply strive to use a large beak gape when producing sound frequencies above ~ 3.5 kHz and strive to use a relatively small beak gape when producing sound frequencies below ~ 3.5 kHz.

We suggest that a decrease in beak gape functions to attenuate the second resonance peak that we observed near ~ 5.5 kHz in all subjects (Figs 1 and 4). Indeed, resonance peaks shown in Fig. 4 were obtained from subjects with a 5 mm beak gape and this resonance peak increases in both width and amplitude as beak gape increases beyond 5 mm (i.e., ~ 4 dB at 11 mm). Subjects may therefore reduce beak gape as a mechanism for decreasing harmonic energy near this resonance frequency (~ 5.5 kHz). As an example, a similar resonance peak and abnormally large beak gape might, in part, explain the example of vocal tract filtering that was described in the canary, *Serinus canaria*, by Hoese et al. (2000 see Fig. 7).

Fletcher and Tarnopolsky (1999) used cylindrical and conical models to estimate the effects of beak gape on radiated sound. Our results are consistent with these models since high sound frequencies tend to radiate more efficiently as beak gape is increased. Moreover, while transfer functions shown in Figs 5 and 6 suggest that a decrease in beak gape might function to attenuate sound frequencies between ~ 4 and 7.5 kHz, increases in beak gape may alternatively amplify these same sound frequencies. For example, resonances within the oral cavity between ~ 4 and 7.5 kHz may combine with resonances near 5.5 kHz that can be attributed to the trachea. Indeed, low-level spectral ripples in our recordings might also be attributed to resonances within the oral cavity (Fletcher and Tarnopolsky, 1999). Finally, and under these latter conditions, it seems possible that songbirds might be able to slightly raise or lower the frequencies that are amplified or attenuated in vocalizations as subjects open and close their beaks. For example, it seems possible that songbirds might be able to modify the overall length and volume of the oral cavity through laryngeal movements and possibly raise or lower the lowest resonance frequency of the oral cavity.

Sound radiation

Directional sound radiation patterns were relatively simple and resemble those reported for the European blackbird (Larsen and Dabelsteen, 1990). As a consequence, we summarize our results using calculations of standard deviation (S.D.). Calculations of S.D. differ from Direction Indices that have been used to summarize directivity patterns in other studies (e.g. Fletcher and Tarnopolsky, 1999). Nevertheless, variation in radiated amplitude is accurately characterized by this calculation and calculations of S.D. can be used to assess how changes in orientation might influence estimates of source amplitude that receivers must make in the absence of reverberations or other cues that might directly indicate a signaler's orientation (e.g. visual cues).

Calculations of S.D. increased between 3 and 3.5 kHz and again near 7 kHz. We do not know what produces these increases in directionality although an increase near 3.5 kHz can be attributed to head size (~ 1.5 to 2 cm diameter), which is roughly equal to wavelength divided by 2π . Indeed, increases in directionality near ~ 3.5 kHz are consistent with calculations of S.D. that we obtained after rotating several wooden spheres with variable diameters around in the same horizontal plane (see

Materials and methods, results not illustrated). Directionality is also likely to vary with body orientation and, potentially, with body size (see Results).

These data are consistent with results reported by Larsen and Dabelsteen (1990) and are also consistent with theoretical predictions (Fletcher and Tarnopolsky, 1999). Measurements of directionality that have been obtained from living birds are also consistent with our results (Brumm, 2002; Nelson, 2000; Witkin, 1977). Interestingly, Witkin (1977) observed a small decrease in chickadee 'B' note amplitudes that were produced with sound frequencies just above 5 kHz and we also observed a slight decrease in directionality near 5 kHz.

Beak gape and sound radiation

Acoustic output above ~ 4 kHz is determined both by orientation and beak gape. As a consequence, it is interesting to consider how these two factors might be related. For example, increases in directionality that occur with beak gape might, in part, explain why relatively high sound frequencies radiate more efficiently as beak gape increases. Nevertheless, the beak functions to attenuate sound frequencies only between ~ 4 and 7.5 kHz and attenuation that occurs as a function of beak gape occurs independently of head and body orientation. As such, additional factors such as resonances within the oral cavity that may be controlled by impedance changes near the beak are certain to eclipse increases in output that may be due to increased directionality. Similarly, it seems likely that directionality depends primarily on relationships between head size, body size and sound wavelength.

Harmonic amplitude and beak movements

Towhees, as well as other species, tend to produce high sound frequencies (>4 kHz) with a large beak gape (>4 mm). This trend can be explained by our data since high sound frequencies would be strongly attenuated if birds were to produce them with a small beak gape (Fig. 5). Conversely, the amplitudes of fundamental frequencies in vocalizations might not be strongly altered if birds were to maintain a relatively large beak gape (>5 mm) over the entire duration of a vocalization (especially below ~ 4 kHz; although see Goller et al., 2004). Why then do towhees and other species produce relatively low sound frequencies (<4 kHz) with a small beak gape?

One possible explanation is that these species produce relatively low sound frequencies (<4 kHz) with a small beak gape as a mechanism for attenuating harmonics with frequencies between ~ 4 and 8 kHz that are generated when birds produce fundamental frequencies between ~ 2 and 4 kHz. Indeed, harmonics with frequencies between ~ 4 and 8 kHz might be especially strong (loud) if birds did not produce fundamental frequencies between ~ 2 and 4 kHz with a small beak gape since sound (harmonic) frequencies between ~ 4 and 8 kHz resonate within the trachea.

Changes in beak gape do not strongly influence low sound frequencies (<3.5 kHz), or midrange sound frequencies between ~ 3.5 and 4 kHz, and towhees tend to produce midrange frequencies with an intermediate beak gape (~ 4 –5 mm). We

suggest that midrange sound frequencies are produced with intermediate beak gapes simply because subjects must, at some frequency, transition between vocalizing with a small and large beak gape (or *vice versa*). That is, if towhees strive to use a relatively small beak gape when producing sound frequencies below ~3.5 kHz and strive to use a large beak gape when producing sound frequencies above ~3.5 kHz, then intermediate values will occur naturally during transitions between these two 'extremes'. Thus, while intermediate beak gapes are commonly observed as vocalizations sweep upwards or downwards through midrange sound frequencies near ~3.5 kHz (e.g. Fig. 12), intermediate beak gapes seem to be observed less frequently when louder or longer sounds are produced in vocalizations with sound frequencies below and above ~3.5 kHz (e.g. Podos et al., 2004).

Implications for communication

Our results suggest that beak gape movements are unlikely to 'track' a wide range of fundamental frequencies in vocalizations in a linear manner (Fig. 1A). Birds clearly vary beak gape while vocalizing and thus our results lead to a slightly different question: why might songbirds benefit from an ability to control the amplitudes of sound frequencies between ~4 and 7.5 kHz?

Changes in beak gape may function to produce species-specific or individual-specific spectral cues. In fact, many songbirds produce frequency components in their vocalizations that exceed ~4 kHz and the amplitudes of these modulations are likely to be strongly influenced by changes in beak gape. Nevertheless, changes in beak gape do not strongly influence sound frequencies below ~4 kHz. In addition, changes in orientation may confound spectral cues that occur above ~4 kHz. As a consequence, changes in beak gape are likely to have additional functions.

Some songbirds have been found to react strongly when played songs with 'pure-tone' syllables (Bremond, 1976; Falls, 1963; Nowicki et al., 1989; Strote and Nowicki, 1996). Harmonics with frequencies above ~7 kHz attenuate rapidly over distance (Nelson, 2003; Wiley and Richards, 1982) and may not be easily detected over relatively long distances (Dooling et al., 2000). Such harmonics may therefore rarely be audible when birds produce fundamentals above ~3.5 kHz (harmonics >7 kHz) in vocalizations. Harmonics may also be inaudible when birds produce lower frequency fundamentals between ~2 and 4 kHz with a small beak gape since sound frequencies (harmonics) between ~4 and 8 kHz are strongly attenuated by the beak.

Towhees rapidly modulate their calls (e.g. Nelson, 2004) and often modulate syllables within their songs even more strongly. Towhees do not therefore seem to vary beak gape as a mechanism for producing pure-tone sounds since these modulations result in 'rough' sounding syllables. Furthermore, while songbirds commonly produce pure-tones in their vocalizations, there are no clear reasons to suspect that a decrease in 'tonality' is the only factor that influences how receivers react when harmonics are experimentally added to

vocalizations (Bremond, 1976; Falls, 1963; Nowicki et al., 1989; Strote and Nowicki, 1996).

Towhees seem to discriminate and modulate sound frequencies above and below ~3.5 kHz differently (Nelson, 2002; Nelson, 2004; Nelson and Suthers, 2004). In addition: (1) sound frequencies above and below ~3.5 kHz often propagate differently over distance (e.g. Nelson, 2003; Wiley and Richards, 1982); (2) several songbirds produce these two frequency ranges using separate sides of their bipartite syrinx (e.g. Suthers, 1999; Suthers and Goller, 1997; Suthers et al., 2004); and (3) female canaries prefer rapid trills that span these same two sound frequency ranges (Vallet et al., 1998). Resonances that we attribute to the trachea would also seem to emphasize sound frequencies to each side of ~3.5 kHz. We therefore propose that towhees vary beak gape as a mechanism for excluding and/or concentrating energy within at least two distinct sound frequency channels and that songbirds may, in general, often produce narrow-band or pure-tone sounds when they achieve this goal.

More specifically, because changes in beak gape alter only the amplitudes of sound frequencies above ~3.5–4.0 kHz, we propose that towhees vary beak gape as a mechanism for preserving the fine (sinusoidal) amplitude envelopes that are imposed upon 'tow-hee' calls by modulations occurring at a rate of ~500 Hz (Nelson, 2004, acoustical changes not illustrated). In addition, we propose that songbirds may, in general, vary beak gape as a mechanism for attenuating harmonics above ~4 kHz so that temporal patterns over these same sound frequencies are not degraded by the harmonics of preceding or subsequent notes (or syllables) that are produced with lower frequencies (<~4 kHz; Fig. 13). Indeed, harmonics between ~4 and 7.5 kHz depicted in Fig. 13A might degrade temporal patterns over these high sound frequencies similarly to the way that environmental reverberations are thought to degrade vocalizations (e.g. Dabelsteen et al., 1993; Wiley and Richards, 1982). Unlike environmental reflections, however, harmonics that are associated with, but not correlated with, preceding or subsequent low frequency components (~2–4 kHz; Fig. 13A) are unlikely to be suppressed by acoustical interactions by neural mechanisms (e.g. Dent and Dooling, 2003a,b). We do not present a natural example of degradation that might be attributed to an abnormally large beak gape. Nevertheless, a clear illustration of this effect was presented by Hoese et al. (2000) in their fig. 7, in which normal temporal patterns across notes with frequencies above ~4 kHz are clearly degraded by abnormal harmonics near the same frequency (~4 kHz, presumably caused by the addition of weights to the beak).

Whether weakly filtered harmonics would normally be strong enough to degrade fine or coarse temporal patterns in vocalizations remains unclear. Nevertheless, changes in amplitude that can be attributed to changes in subject orientation and beak gape occur primarily above ~4 kHz and these changes may help to explain why towhees use attenuation (amplitude) as a distance cue only when listening to sound frequencies below ~3.5 kHz (Nelson, 2002). The reason being that attenuation could not function as a reliable distance cue if signalers were

able to vary beak gape or orientation and alter what otherwise seems to be a reliable relationship between distance and attenuation (where attenuation is proportional to distance and equal to source amplitude minus incident amplitude). These results do not explain why towhees sometimes vocalize with a small beak gape (although see Goller et al., 2004), but do suggest that towhees may pay attention to different dynamic variables when hearing sound frequencies below or above ~3.5 kHz.

How towhees vary beak gape while singing is not expected to differ markedly from other songbird species (e.g. Hoese et al., 2000; Podos et al., 2004; Westneat et al., 1993). Indeed preliminary analyses suggest that introductory syllables in towhee songs with sound frequencies below ~3.5–4.0 kHz are produced with a relatively small beak gape (0–4 mm) while sound frequencies between ~4 and 7.5 kHz are produced with a relatively wide range of beak gapes (0–11 mm). In addition, while it seems possible that songbirds might be able to slightly raise or lower the frequencies of resonances that are associated with the oral cavity (see above), there are no clear reasons to presume that different sounds or vocalization types will resonate differently within the vocal tract (e.g. synthetic frequency sweeps, calls or songs).

In conclusion, we propose that songbirds vary beak gape as a mechanism for excluding and/or concentrating energy within at least two distinct sound frequency ‘channels’, where a channel is defined as the proportion of a frequency spectrum that is used for a specific purpose. We further propose that achieving this goal avoids degrading temporal patterns and that narrow-band sounds are produced in vocalizations when songbirds achieve this more ostensible goal. We do not quantify the dynamics with which towhees vary beak gape when producing rapid trills in songs. Nevertheless, prior results (Hoese et al., 2000) suggest that towhees may need to rapidly modulate the gapes of their beaks in order to maintain temporal clarity across notes that are produced with frequencies above ~3.5–4.0 kHz.

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