Radiation efficiency for long-range vocal communication in mammals and birds

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(Received 23 January 2018; revised 9 April 2018; accepted 11 April 2018; published online 11 May 2018)

Long-distance vocal communication by birds and mammals, including humans, is facilitated largely by radiation efficiency from the mouth or beak. Here, this efficiency is defined and quantified. It depends on frequency content of vocalization, mouth opening, head and upper body geometry, and directionality. Each of these factors is described mathematically with a piston-in-a-sphere model. While this model is considered a classic, never before has the high frequency solution been applied in detail to vocalization. Results indicate that frequency content in the 1–50 kHz range can be radiated with nearly 100% efficiency if a reactance peak in the radiation impedance is utilized with adjustments of head size, mouth opening, and beam direction. Without these adjustments, radiation efficiency is generally below 1%, especially in human speech where a high fundamental frequency is a disadvantage for intelligibility. Thus, two distinct modes of vocal communication are identified, (1) short range with optimized information transfer and (2) long range with maximum efficiency for release of acoustic power. © 2018 Acoustical Society of America.

<https://doi.org/10.1121/1.5034768>

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Pages: 2813–2824

I. INTRODUCTION

Many birds and mammals, including humans, have adapted their sound producing mechanisms for different communication objectives. In long range vocalization, maximum propagation distance is achieved, mostly by maximizing sound power radiated to the listener (Fletcher, 2007). In short range vocalization, sound complexity is increased for maximum information transfer to the listener (Shannon, 1948; Reed and Durlach, 1998; Fletcher, 2009). The two adaptations drive the fundamental frequency of vocalization in opposite directions, low f_0 for maximum information transfer and high f_0 for maximum radiated power (Gridi-Papp, 2008; Wilkins *et al.*, 2013; Pasch *et al.*, 2017). They also determine the nature of the modulations imposed on the sound carrier. Some species have acquired both communication modes, one with a strong high-frequency carrier and less modulation complexity for long distance communication, and another with a low frequency carrier and extended modulation complexity for short-range social interaction (Janik and Slater, 2000; Riede *et al.*, 2016; Pasch *et al.*, 2017).

Sound transmission loss along varied ground surfaces diminishes rapidly with height from the ground (Naguib and Wiley, 2001). Attenuation in the upper forest strata is low in the frequency range between 100 and 1000 Hz (Whitehead, 1987; Zuberbühler *et al.*, 1997). Hence it has been hypothesized by some that this particular frequency range is most

suitable for long distance communication (Zuberbühler *et al.*, 1997). However, many species of mammals and birds use much higher frequency components, well above 5000 Hz, for long-distance communication. Examples are chimpanzee screams (Mitani and Nishida, 1993; Notman and Rendall, 2005), components in the roars of Howler monkeys (Sekulic, 1982; Whitehead, 1995), howls of wolves (Theberge and Falls, 1967), and coyotes (McCarley, 1975), bugles of elks (Feighny *et al.*, 2006; Riede and Titze, 2008), screaming of piha birds (Fitzsimmons *et al.*, 2008), bonks of three-wattled bellbirds (Kroodsma *et al.*, 2013), and alarm calls of American pikas (Broadbooks, 1965; Conner, 1982). A common feature for these loud high-frequency calls is that they are produced with wide-open mouths (Fig. 1).

Directivity of sound radiation is also part of long-range communication. Frommolt and Gebler (2004) studied directionality of dog vocalizations in long-distance signals. They observed an increase in difference of sound pressure level between forward and backward directions with increase in frequency. Jakobsen *et al.* (2013) studied the intensity and directionality of bat echolocation signals. They used a piston in an infinite baffle model to study directionality and suggested that intensity and directionality increases with frequency. Directionality of avian vocalization was studied by Hunter *et al.* (1986) using a piston in a sphere model and laboratory experiments. They also suggested that directionality is strongly dependent on frequency and found that it is profound in the horizontal and sagittal planes but not in the transverse plane.

Fletcher (2004) reasoned that the optimum frequency for transmission over a given distance is based on a trade-off between radiated power from the source and the frequency-dependent transmission loss through the medium between

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FIG. 1. (Color online) An American pika (*Ochotona princeps*) whistling from a rock for long-range communication. Photo courtesy of David Kingham.

the source and the receiver. He concluded that the optimum vocalization frequency was proportional to $M^{-0.4}$, where M is the mass of the animal. Given that the radiated acoustic power is proportional to the square of the frequency (Morse, 1976), the optimal frequency is therefore predictable by animal size. However, there is large variability because it is also affected by specific mouth, head, vocal fold, and airway anatomy. Radiated power rises dramatically when the wavelength of the sound is on the order of the diameter of the mouth or beak (Morse and Ingard, 1968; Morse, 1976; Bradbury and Vehrenkamp, 1998).

At low to moderate frequencies, most of the sound generated by the source (larynx or syrinx) is not radiated efficiently from the airway opening (mouth, beak, or nostrils). For human speech, for example, the efficiency of converting aerodynamic power to radiated acoustic power is on the order of 0.01% to 1.0% (Schutte, 1980). Most of the aerodynamic power generated by the lungs is not converted to acoustic power, and most of the acoustic power is dissipated in the airway walls (Titze *et al.*, 2016) because sound reflection at the mouth is very high. At high frequencies, however, two physical factors can be invoked, a large mouth or beak opening and the effective use of body surfaces as a baffle. Both factors affect the amount of acoustic energy released into free space from a sound source embedded in an airway. Bradbury and Vehrenkamp (1998) have given a thorough phenomenological description of the physics of sound radiation from a spherical source in terms of monopole, dipole, and quadrupole patterns. They introduced the concept of radiation efficiency, but gave no formula for computing it. They suggested that radiation efficiency increases monotonically with frequency and saturates close to 100% when the wavelength of the sound is of the same size or smaller than the diameter of the sound source.

Bradbury and Vehrenkamp (1998) gave an air-particle based description of radiation impedance and reactance, showing clearly how resistance and reactance change with wave number $\omega c/a$, where a is the radius of the oscillating surface of (or part of) a sphere. The transformation of the impedance from series to parallel elements was not included in their discussion, however. By extending the radiation

model, we show here how an animal might position its head, and to some degree its entire body, for long-range vocalization. While the acoustic principles underlying our approach have been described mathematically by Morse and Ingard (1968) and phenomenologically by Bradbury and Vehrenkamp (1998) and Fletcher (2007), the definition and quantification of radiation efficiency for specific applications have not been treated formally.

II. THEORETICAL BACKGROUND AND DEFINITION OF RADIATION EFFICIENCY

Sound radiation from the mouth, beak, or nostrils in vocalization is often modeled by an oscillating piston in a spherical baffle (Morse, 1976; Flanagan, 1972). The sphere represents the head, or part of the upper body if the head is retracted (Fig. 1), and the piston represents the air oscillating at the mouth. This model has not been challenged for human vocalization and has also been applied to other vertebrate species like birds (Hunter *et al.*, 1986; Fletcher *et al.*, 2006). Mathematically, the radiation impedance (defined as acoustic pressure divided by air particle velocity at the mouth) can be expressed in terms of two low-frequency lumped impedance elements, a *radiation resistance* in parallel with a *radiation inductance*. For nearly a century, it has been assumed that this low frequency lumped-element impedance approximation is valid up to several kHz, but the exact cutoff frequency has rarely been specified because it depends on the head size and mouth opening (Morse and Ingard, 1968). In this paper, we provide both the validity of the approximation and cases for which there is a sharp departure. In human speech, for example, limited mouth opening, a neck that separates the head baffle from the body baffle, and low fundamental frequency are the main contributors to low vocal efficiency. Other species can avoid this low efficiency with higher fundamental frequency and body posturing.

Vocal efficiency can be divided into three components, (1) conversion efficiency from aerodynamic to acoustic power, producing an acoustic glottal flow, (2) transmission efficiency through the airways, and (3) radiation efficiency from a surface or an opening (Fig. 2). Here, we quantify only the radiation efficiency component. We offer a definition of radiation efficiency and show that it is generally on the order of 1% or less at low fundamental frequencies. However, radiation efficiency rises dramatically above

FIG. 2. Sound production at glottis, transfer through the airway, and radiation from the mouth.

1 kHz with wide mouth openings in non-speech vocalizations such as screaming, singing, calling, and laryngeal whistling. The work of Fletcher *et al.* (2006) and Riede *et al.* (2006) on bird vocalization showed how radiation efficiency can be raised in singing and calling by cancelling part of the *radiation inductance* with a pharyngo-esophageal air sac compliance. In this article, we show an alternative solution for species that do not have a pharyngo-esophageal air sac, yet communicate vocally over large distances. Use is made of a resonance peak in the *parallel radiation inductance* that prevents the shunting away of acoustic airflow at the mouth that could be radiated. If the fundamental frequency or a harmonic frequency is in the 1–50 kHz range, the shunting effect can be nearly eliminated to obtain nearly 100% efficient radiation. The combination of an air sac with this radiation resonance is left for a future investigation.

Figure 3 shows the Morse and Ingard (1968) model of acoustic radiation from a piston (the mouth) driving air back and forth in a spherical baffle (the head in combination with the upper body). A series radiation impedance z , defined as the acoustic pressure divided by the air particle velocity at the mouth opening of radius a_p , depends on the sphere radius a and a gape half-angle ϑ . It was derived analytically by Morse and Ingard as

$$z = \rho c(r + ix), \quad (1)$$

where ρ is the air density, c is the sound velocity in air, r is a normalized acoustic resistance, x is a normalized acoustic reactance, and $i = \sqrt{-1}$. This impedance generally does not match the impedance of a wave propagating through the airway in the body, which means that most of the acoustic energy produced at the larynx or syrinx gets reflected back upon itself at the mouth opening. Both wave reflection and wave radiation can be quantified by a simple lumped-element “flow circuit” approximation of z (Flanagan, 1972). This results in a *radiation resistance* R_r in parallel with a *radiation inductance* I_r as shown in Fig. 4,

$$R_r = \rho c(r + x^2/r), \quad (2)$$

FIG. 3. Piston of radius a_p embedded in a sphere of radius a with a piston half-gape angle θ (after Morse, 1976).

FIG. 4. Parallel resistance-inductance acoustic radiation circuit.

$$I_r = \rho c(x + r^2/x)/\omega, \quad (3)$$

where ω is the angular frequency. In the acoustic radiation circuit of Fig. 4, U is the mouth airflow, and U_i and U_r are airflows through the parallel elements. (Inside the airway, air movement is often described in terms of volume flow rather than particle velocity.) The pressure P is the radiated acoustic pressure. The power radiated is $U_r^2 R_r$, which increases when less airflow is shunted through the inductance element I_r . Thus, the radiated power is maximized when I_r becomes very large, meaning that U_i goes to 0, U_r equals U , and the radiation impedance is no longer reactive to the mouth airflow.

The current theoretical development began with recalculating the analytical Bessel function solutions of Morse and Ingard (1968) for r and x in Eq. (1). The series resistance and reactance are plotted as a function of wave number $\mu = \omega a_p / c$, where ω is the angular frequency. The solutions depend on the gape opening half-angle ϑ , illustrated above in Fig. 3. This angle relates the piston (mouth) radius a_p to the sphere (head) radius a . The analytical expressions for r and x are infinite series of Bessel functions, the mathematics of which we reproduced. Four values of ϑ were chosen, as in Morse’s work, but an angle of 2° was used instead of 0° to reflect a small mouth opening rather than no mouth opening. Figure 5 shows the re-calculations plotted against wave number μ .

According to Fig. 3, the two radii are related to each other through the gape half-angle ϑ , such that

$$a_p = a \sin(\vartheta), \quad (4)$$

but to bring the flat surface of the piston into equivalence with a spherical cap surface, Morse and Ingard defined an effective radius by using the formula of a spherical cap surface area

$$A = 2\pi a^2(1 - \cos \vartheta) = 2\pi a^2[2 \sin^2(\vartheta/2)], \quad (5)$$

from which the *effective radius* of the piston became

$$a_p = 2a \sin(\vartheta/2). \quad (6)$$

The series resistance-reactance pair (r, x) is converted to a parallel resistance-reactance pair (R, X) by using complex algebra,

FIG. 5. (Color online) Normalized series radiation resistance (A) and reactance (B) versus wave number for several gap half-angles (after Morse, 1976).

$$\frac{R(iX)}{(R + iX)} = r + ix, \quad (7)$$

which yields

$$R = r + x^2/r, \quad (8)$$

$$X = x + r^2/x. \quad (9)$$

The normalized series r and x curves were numerically converted to parallel R and X curves for the four angles (2° , 20° , 40° , and 60°). For the current analysis, a_p and ω were separated from the wave number such that frequency was taken as the independent variable and a_p became a separate parameter. The dependent variables of interest became the dimensional values of the parallel radiation resistance R_r and the parallel radiation inductance I_r (Fig. 4), namely,

$$R_r = \rho c R, \quad (10)$$

$$I_r = \rho c X / \omega, \quad (11)$$

which are Eqs. (2) and (3). When volume flows are used instead of particle velocities in voice simulation, the resistance and inductance in Eqs. (10) and (11) need to be divided by the piston area πa_p^2 .

A. Frequency variation of parallel elements

The frequency variations of the parallel resistance R_r and the parallel inductance I_r are shown in Fig. 6 for a 0.5 cm mouth radius (A and C) and a 3.0 cm mouth radius (B and D). Note the constancy with frequency up to about 5 kHz for the 0.5 cm radius and to about 1 kHz for the 3.0 cm radius. The families of curves represent different gap half-angles (2° , 20° , 40° , and 60°), which in turn depend on baffle size (head and upper body). There is a non-monotonic relation with ϑ . The 0° and 40° curves are in the center of the family and the 2° and 60° curves are at the extremes. If an average human head radius of 9.0 cm is assumed, the gap half-angle ϑ is 3.2° for $a_p = 0.5$ cm, near the 2° curve, according to Eq. (6). The gap half-angle is 19° for $a_p = 3.0$ cm, near the 20° curve, which is at the top of the family. For the 3.0 cm mouth opening, the non-constant regions of R_r and I_r move to the left (downward in frequency). Significant variation of the inductance I_r (lower graphs) is seen by two peaks at about 30 kHz for $a_p = 0.5$ cm and at about 5 kHz for $a_p = 3.0$ cm. These peaks can be used to dramatically increase radiation efficiency, as will be seen.

Note the 6:1 vertical scale change from left (C) to right (D) in the bottom panels of Fig. 6. For a change from 0.5 cm mouth radius to 3.0 cm mouth radius, the overall inductance is

FIG. 6. (Color online) Parallel resistance [(A) and (B)] and inductance [(C) and (D)] as a function of frequency, mouth radius (left-right), and gap half-angle (family of curves).

increased by a factor of 6. In addition, the frequency for which the inertance reaches two peaks is lowered by a factor of 6. These peaks in the inertance are not likely to be important in most human speech and some singing, but harmonics significantly above 1 kHz could be affected. For screaming, or high frequency whistle voice, humans may make use of these inertance peaks. Birds and small mammals may utilize them regularly.

The low-frequency asymptotic values for the resistance and inertance are given by Morse (1976) and Flanagan (1972) for a 0° gape half-angle,

$$R_r = 128\rho c/(9\pi^2) = 57.46 \text{ g}/(\text{cm}^2 \text{ s}), \quad (12)$$

$$I_r = 8a_p\rho/(3\pi) = 0.9677a_p \text{ mg}/\text{cm}^2. \quad (13)$$

These equations show explicitly that the inertance is directly proportional to the mouth radius while the resistance is independent of mouth radius. For this 0° gape half-angle approximation, the spherical baffle effectively becomes an infinite plane baffle (a huge head or upper body). These low-frequency 0° approximations have been used almost exclusively in speech simulation over the entire frequency range, primarily because the resistance drops only from 57.46 g/(cm² s) = 1.44 ρc at zero frequency to 39.9 g/(cm² s) = ρc at 100 kHz. However, the high-frequency peaks in the inertance present order-of-magnitude deviations from the low-frequency approximation.

B. Definition of radiation efficiency

Radiation efficiency is defined and calculated here as the ratio of the power radiated divided by the power delivered to the mouth, which according to Fig. 4 can be written as

$$E_r = \frac{U_r^2 R_r}{\int P U dt}. \quad (14)$$

As stated, maximum efficiency occurs when the entire mouth flow U becomes U_r (i.e., when the flow through the inertance $U_i = 0$). For a single-frequency sinusoidal airflow, where the phase of U is taken to be zero (reference phase) and complex phasor notation is used for U_i and U_r , the efficiency is

$$\begin{aligned} E_r &= \frac{U_r U_r^* R_r}{U^2 R_r} = \frac{(U - U_i)(U - U_i)^*}{U^2} \\ &= \left(1 - \frac{U_i}{U}\right) \left(1 - \frac{U_i}{U}\right)^*, \end{aligned} \quad (15)$$

where the asterisk represents a complex conjugate operation. From flow continuity $U = U_i + U_r$ and a pressure equivalence $P = R_r U_r = i\omega I_r U_i$ we obtain

$$\frac{U_i}{U} = \frac{R_r}{(R_r + i\omega I_r)}. \quad (16)$$

After some complex algebra to rationalize the denominator in Eq. (16), the result for radiation efficiency becomes

$$E_r = \frac{(\omega^2 I_r^2)}{(R_r^2 + \omega^2 I_r^2)}. \quad (17)$$

Equations (14) and (17) are the key mathematical relations for computation of radiation efficiency as a function of frequency and mouth radius. Note that radiated power is proportional to the square of frequency ω as well as the square of the parallel inertance I_r , which translates to the square of the mouth radius. Species that can produce frequencies above 1 kHz with a large mouth (or beak) opening may rely on the inertance peaks to boost radiation efficiency.

Equation (17) is an on-axis magnitude calculation on the surface of the sphere. Figure 7 shows radiation patterns for three frequencies, 0.9, 4.6, and 8.3 kHz. The spherical grid lines represent constant vocal intensity. For all the three cases, the head radius is 9.0 cm, the gape half-angle is approximately 20°, and the mouth radius is 3 cm. The curves represent radiation intensity measured on the surface of the sphere based on the equations given in Morse and Ingard (1968). Note that off-axis, the intensity diminished considerably for higher frequencies. The radiation changes from symmetrical to directional as the frequency increases. The intensity is very small for frequencies below 1 kHz (not clearly visible in Fig. 7 but can be seen in the Appendix, Fig. 11). The intensity rises considerably near the first peak in the inertance curves. However, the intensity along the axis does not increase monotonically with frequency. There is an initial frequency range for which the intensity increases gradually along the axis, depending on the head size and mouth radius. After reaching a peak, it falls off dramatically. The intensity increases and decreases periodically along the axis with increase in frequency. Radiation directivity patterns for more cases are shown in the Appendix. It can be observed

FIG. 7. (Color online) Radiation patterns for a head radius of 9.0 cm and a gape half-angle of 20°, which yields a mouth radius of 3 cm. f_o at 4.6 kHz is near the first peak in the inertance curve in Fig. 6 bottom right panel. f_o at 8.3 kHz is near the first trough in the inertance curve in Fig. 6 bottom right panel.

FIG. 8. (Color online) [(A) and (B)] Radiation efficiency as a function of frequency for two mouth radii, and [(C) and (D)] radiation efficiency as a function of mouth radius for two frequencies. Solid lines are for sinusoidal mouth flow and dashed lines are for sawtooth mouth flows with different sampling rates.

that the radiation beam becomes narrower with increase in frequency, along with sustained increase in the number of side lobes.

III. METHODS AND RESULTS FOR LOW-FREQUENCY EFFICIENCY CALCULATIONS

Assuming the typical low-frequency asymptotes chosen for resistance and inertance in Eqs. (12) and (13), respectively, the radiation efficiency for sinusoidal flows was calculated from Eq. (17), with mouth radius and frequency being independent variables. The solid curves at the top (A and B) of Fig. 8 show efficiency versus frequency for two different mouth radii, whereas at the bottom (C and D) the solid curves show efficiency versus mouth radius for two different frequencies (200 and 5000 Hz). The dashed lines are for the sawtooth waveforms with different sampling frequencies, to be discussed below.

From the solid lines it can be seen that the radiation efficiency is generally very low (below 1%) for small mouth radii and frequencies below 1 kHz, but can approach 100% for frequencies above 10 kHz and large mouth radii. At speech fundamental frequencies (around 200 Hz, bottom left graph), the radiation efficiency for a sinusoid is less than 1% (solid line) for all mouth radii. At 5 kHz, 70% efficiency is

achievable for large radii. [Note that the efficiency scale has been changed from 0% to 80% on the right to 0% to 6% on the left.]

To compute the radiation efficiency for non-sinusoidal mouth flow with harmonic components, a sawtooth-wave airflow U was applied to the parallel circuit in Fig. 4 and the differential equation for $P = U_r R_r = I_r dU_i/dt$ and the flow continuity equation $U = U_i + U_r$ were solved numerically with a fourth order Runge-Kutta solver. Figure 9 shows the simulated waveforms for the flows U , U_i , U_r , and the radiated pressure P . The contrast between sinusoidal and sawtooth waveforms for mouth flow was chosen because they represent two extremes in harmonic content, none for the sinusoid and a -6 dB/octave harmonic amplitude decay for the sawtooth. Normal mouth flows in phonation usually have spectral decays varying between -6 dB/octave and -24 dB/octave (close to a sinusoid).

Note that for this ideal sawtooth function, the radiated pressure P and the radiated flow U_r are impulses. In normal voice production, the shut-off of the mouth flow will be more gradual, resulting in a pulse width for U_r and P .

The radiation efficiency for the sawtooth was calculated with root-mean-squared (RMS) values of U and U_r from the original efficiency definition [Eq. (14)]

FIG. 9. (Color online) Simulated waveforms U , U_i , U_r , and P for a 200 Hz sawtooth-wave mouth flow and a mouth radius of 0.5 cm.

TABLE I. Fourth-order z- transform coefficients for radiation resistance at 0.5 cm mouth radius.

θ	b_0	b_1	b_2	b_3	b_4	a_0	a_1	a_2	a_3	a_4
2°	43.9623	-60.9563	52.6901	-24.2075	5.2575	1.0000	-1.5474	1.3394	-0.6456	0.1446
20°	44.5787	-73.6180	59.9054	-27.8737	5.1048	1.0000	-1.8405	1.5502	-0.7409	0.1459
40°	43.1536	-88.3433	81.4831	-43.9702	10.8080	1.0000	-2.1798	2.0812	-1.1384	0.2943
60°	42.2635	-80.0799	69.6515	-35.4575	8.0881	1.0000	-1.9875	1.7761	-0.9085	0.2166

$$E_r = \frac{U_r^2 R_r}{U^2 R_r}. \quad (18)$$

Returning to Fig. 8, the dashed lines show efficiency calculations for a sawtooth mouth flow with two different sampling frequencies. Given the sharp decline of the sawtooth wave and the sensitivity of the efficiency calculation to high frequencies, sampling rate is a major consideration. Radiation efficiency was calculated using two sampling rates: 200 000/(2 a_p) labeled as Sawtooth1, and 1 000 000/(2 a_p) labeled as Sawtooth2. The estimated values of efficiency are higher for the higher sampling rate due to the inclusion of more frequencies in the computation of efficiency. The frequency content in natural phonations is limited, of course, as is the hearing range of all species. Hence, the sampling frequency should be guided by these natural constraints.

The bottom left panel (C) of Fig. 8 shows the radiation efficiency for this sawtooth mouth flow (dashed line) at a fundamental frequency typical in speech (200 Hz). For this low fundamental frequency, the spectral content of the sawtooth mouth flow is very important for raising the radiation efficiency, even when only the low-frequency approximation is used for the radiation impedance. It is also shown that the radiation efficiency rises from below 1% to nearly 4% as the mouth radius increases from 0.5 to 3.0 cm. The harmonic content is less important at high fundamental frequencies (bottom right) because only a few harmonics of the sawtooth reside in the reactance peaks. Note that the dashed lines do not differ much from the solid line.

IV. METHODS AND RESULTS FOR HIGH-FREQUENCY EFFICIENCY CALCULATIONS

The high-frequency variation of the parallel resistance and inertance in Fig. 6 were curve-fitted with a fourth-order z-transform of the transfer functions $R_r = P/U_r$ and $I_r = P/(dU_r/dt)$,

$$H_R(z) = \frac{b_0 + b_1 z^{-1} + b_2 z^{-2} + b_3 z^{-3} + b_4 z^{-4}}{a_0 + a_1 z^{-1} + a_2 z^{-2} + a_3 z^{-3} + a_4 z^{-4}}, \quad (19)$$

TABLE II. Fourth-order z-transform coefficients for radiation inertance at 0.5 cm mouth radius.

θ	b_0	b_1	b_2	b_3	b_4	a_0	a_1	a_2	a_3	a_4
2°	0.0008	0.0003	0.0002	0.0000	-0.0001	1.000	0.3767	0.5885	0.3048	0.3323
20°	0.0006	0.0000	0.0002	-0.0001	0.0000	1.000	0.0734	0.4559	0.0257	0.1169
40°	0.0004	-0.0001	0.0002	-0.0001	0.0000	1.000	-0.1887	0.4839	-0.1492	0.0713
60°	0.0004	-0.0003	0.0003	-0.0002	0.0001	1.000	-0.6939	0.7745	-0.4684	0.2232

$$H_I(z) = 2a_p \frac{b_0 + b_1 z^{-1} + b_2 z^{-2} + b_3 z^{-3} + b_4 z^{-4}}{a_0 + a_1 z^{-1} + a_2 z^{-2} + a_3 z^{-3} + a_4 z^{-4}}. \quad (20)$$

The coefficients for the resistance and inertance for an effective piston radius of 0.5 cm are shown in Tables I and II, respectively, for all the four gape half-angles. The two peak frequencies in the inertance curves as a function of a_p are given by

$$f_1 = \frac{36.21 \text{ kHz cm}}{2a_p}, \quad f_2 = \frac{72.42 \text{ kHz cm}}{2a_p}. \quad (21)$$

In order for the coefficients to apply to any piston area, the sampling rate for the z-transform needs to vary with mouth opening,

$$F_s = \frac{100 \text{ kHz cm}}{a_p}. \quad (22)$$

This inverse relation between sampling frequency and mouth radius calls for a sampling frequency of 200 kHz for a piston radius of 0.5 cm and a sampling frequency of 33.3 kHz for a piston radius of 3.0 cm. The coefficients in Eqs. (19) and (20) are then valid for frequencies up to half of the sampling frequency.

Figure 10 shows on-axis radiation efficiency when the high-frequency variation in R_r and I_r described above are included. The curves in Figs. 10(A) and 10(B) are for a sinusoidal mouth flow computed analytically with Eq. (17), while the curves in Figs. 10(C) and 10(D) are for a sawtooth mouth flow computed digitally with Eq. (18). The parameter in the family of curves is the gape half-angle. The left panels (A and C) in Fig. 10 are for a 0.5 cm mouth radius and the right panels (B and D) are for 3.0 cm mouth radius.

Note that sinusoids (upper curves) can be radiated with nearly 100% efficiency at 30 kHz with a small mouth radius (0.5 cm) and at about 5 kHz with a large mouth radius (3.0 cm). The variations with gape half-angle are not very large for sinusoids. However, for sawtooth waves (bottom curves), the spread is larger with gape half-angle because harmonic frequencies near the inertance peaks are radiated

FIG. 10. (Color online) Radiation efficiency as a function of frequency for [(A) and (B)] sinusoidal mouth flow and [(C) and (D)] sawtooth mouth flow for a 0.5 cm mouth radius and a 3.0 cm mouth radius and four gape half-angles.

selectively and differently. It can be observed that a smaller gape half-angle has greater efficiency, suggesting that for a given mouth radius, a larger baffle (head or body) is beneficial for efficient sound radiation.

The efficiency curves for sawtooth mouth flows would all approach 100% if an infinite number of harmonic frequencies were included in the digitally sampled waveforms. The sampling frequency limits this high efficiency, however. In our digital filter implementation, the sampling frequency F_s for the sawtooth curves was based on mouth opening, as explained. F_s was 200 kHz for a mouth radius of 0.5 cm, which included frequencies up to 100 kHz. F_s was 33 kHz for a mouth radius of 3 cm, which included frequencies up to 16.5 kHz. Thus, for a 5 kHz fundamental, only 20 harmonics were included with 200 kHz sampling and only 3 harmonics were included with 33 kHz sampling. Digital computations of radiation efficiency with complex mouth airflows require careful selection of the sampling frequency.

It is interesting to note that efficiencies on the order of 10% to 50% can be reached in the 1–5 kHz fundamental frequency range with harmonically-rich mouth waveforms such as a sawtooth. For example, with a 3.0 cm radius, a 1 kHz fundamental with two additional harmonics [Fig. 10(D)] can yield up to 20% efficiency, while less than 10% can be reached with a pure sinusoid [Fig. 10(B)]. As stated, the difference comes from the fact that multiple harmonics can benefit from the increased radiation efficiency when the mouth flow waveforms are complex.

V. DISCUSSION AND CONCLUSIONS

Radiation efficiency has been shown to be a crucial component of long-range vocal communication, a necessity for survival for many birds and mammals. A high fundamental frequency is the most important factor, followed by mouth opening, head and body posturing, and direction of sound propagation. Behavior of mammals and birds during long-distance vocal communication validates these results. Callers tend to open their mouths or beaks wide, cock their heads back to use their body as a baffle and raise fundamental frequency. As mentioned in Sec. I, it has been validated

here that animal size and mass are not the only factors in deciding optimal fundamental frequency for long-distance vocal communication. The significantly greater radiation efficiency achieved with fundamental frequencies above 1 kHz weighs above the observation that 100–1000 Hz frequencies are ideal for long-range communication due to low transmission losses. Experimental studies on eastern towhee, *Pipilo erythrophthalmus* L. (Nelson *et al.*, 2005) showed that reducing the beak gape reduces the amplitude of sound frequencies above 4 kHz.

Supporting this new finding, many loud, high-frequency calls of mammals and birds are observed to be above 1 kHz in frequency (Passilongo *et al.*, 2010; Gerhardt, 1976; Zuberbühler *et al.*, 1997). The whistle portion of the elk bugle has fundamental frequencies up to 2.5 kHz (Feighny *et al.*, 2006; Riede and Titze, 2008). The piha bird scream can reach up to 5 kHz (Fitzsimmons *et al.*, 2008); the three-wattled bellbird calls between 2 and 4 kHz (Saranathan *et al.*, 2007); the American pika uses short calls between 750 and 1000 Hz (Hafner and Smith, 2010) but has several strong harmonics above 1 kHz (Conner, 1982; Ivins and Smith, 1983). The climax scream of the pant-hoots of chimpanzees have a fundamental frequency of about 1 kHz with rich harmonic content (Clark and Wrangham, 1993; Riede *et al.*, 2004; Slocombe and Zuberbühler, 2005).

As a specific example, consider the Piha bird (*Lipaugus vociferans*), which has a song that ends in a scream, gliding to 5 kHz with a sound level that rivals that of a professional singer (110 dB at 1 m distance according to Nemeth, 2004). It retracts its head during the scream so that the entire body becomes the baffle, with its beak wide open. Thus, the bird maximizes the beak opening to lower the frequency of the inertance peaks. It likely also adjusts the effective gape angle with a full body baffle to make optimal use of the magnitude of the peak inertance. Finally, if it directs its sound at an angle suitable for its target, likely considering its tree height above the ground, the radiation efficiency can approximate 100%.

As an example of human singing, consider a female producing a whistle voice at 3 kHz with a 1.5 cm mouth radius. According to Eq. (21), the inertance peaks will be at 12.07

and 24.14 kHz with gape half-angle of about 10° . The peak inertance will be 5.1 mg/cm^2 . The radiation efficiency according to Eq. (18) will be 11.2% for the fundamental and 38.3% for a second harmonic.

To the contrary, if human vocalization is primarily in the form of speech, where the fundamental frequency is on the order of 100–300 Hz, the radiation efficiency for all mouth openings and gape angles is on the order of 4% or less in Fig. 8. Most of the acoustic energy produced in the larynx remains in the airway. Given the head and neck anatomy of humans, little can be adjusted to change the radiation efficiency other than raising the fundamental frequency dramatically. This is contrary, however, to the need to maintain speech intelligibility, which uses airway resonances for phonemic distinction. Resonance frequencies for vowels and consonants would be poorly energized, or not energized at all, if fundamental frequencies were in the range of 1–5 kHz. Thus, our data indicate that there is an inherent conflict between speech intelligibility and radiation efficiency.

Animals benefit from omnidirectional radiation when the target location is not known and needs to be communicated with conspecifics (Yorzinski and Patricelli, 2009). From the current study, it can be observed that animals can achieve omnidirectional radiation at low frequencies. However, the intensity of radiated sound is very low for omnidirectional radiation and can only be heard at small distances. On the other hand, animals use directionality of sound radiation to avoid the risk of being detected by unwanted listeners (Larsen and Dabelsteen, 1990) and also to focus the intensity in the desired direction to wanted listeners. In the current study, we have shown that vocal intensity does not increase monotonically with increase in frequency along the beam axis. There will be an optimal frequency where the vocal intensity is large and directed along specific angles, depending on head and mouth radius. This finding was also observed from the directional acoustic radiation experiments on male sage grouse *Centrocercus urophasianus* (Dantzker et al., 1999). They observed a deep null directly in front of the bird in the beam pattern of the whistle note but not at other frequencies above or below it.

For any vocalizations with high f_o , it has been shown that a simple lumped-element flow circuit approximation for

the radiation impedance can be used up to 5 kHz for relatively small mouth openings, but the accuracy is improved if the frequency dependencies of the resistance and the inertance are included, especially if there is high harmonic content in the mouth flow. For time-domain simulation, various z-transform approaches can be used. Our choice of a fourth-order z-transform required a sampling frequency that varies with lip opening if the coefficients of the transform are to be kept constant. This is a drawback if lip opening is dynamically varying, as in speech. Fortunately, long-distance vocalizations rarely include much lip or beak movement, which softens the drawback.

The primary limitation of the current study is that the theory is not backed by direct radiation efficiency measures in mammals or birds, either in the laboratory or in the field. The computational results are backed only by behavioral analysis of animals such as mouth opening, head posturing, and raising fundamental frequency during long-distance vocal communication or through experimental evidence from acoustic radiation measurements in animals. It will be interesting to calculate the true radiation efficiency of mammals and birds during long-distance vocal communication by conducting experiments in a laboratory setting. The primary question of interest is whether animals maximize radiation efficiency for long-distance vocal communication or limit themselves to lesser values by also adjusting the sound volume due to other factors such as the presence of predators, size of habitat, or distance to the receiver.

ACKNOWLEDGMENT

Support for this research was provided by NIH NIDCD Grant No. R01 DC013573.

APPENDIX

The radiation patterns for progressively increasing frequencies are shown in Fig. 11. The circular grid lines indicate constant radiation intensity. It can be observed that the directionality increases with increase in frequency. The width of the main lobe decreases and the number of side-lobes increases with increase in frequency. The intensity of

FIG. 11. Radiation patterns on the surface of the sphere for different frequencies.

FIG. 12. (Color online) Radiation resistance as a function of frequency for a 0.5 cm mouth radius and four mouth opening angles. Solid lines are for analytical calculations and dashed lines are for digital filter approximations.

FIG. 13. (Color online) Radiation resistance as a function of frequency for a 3.0 cm mouth radius and four opening angles. Solid lines are for analytical calculations and dashed lines are for digital filter approximations.

FIG. 14. (Color online) Radiation inductance as a function of frequency for a 0.5 cm mouth radius and four opening angles. Solid lines are for analytical calculations and dashed lines are for digital filter approximations.

FIG. 15. (Color online) Radiation inductance as a function of frequency for a 3.0 cm mouth radius and four opening angles. Solid lines are for analytical calculations and dashed lines are for digital filter approximations.

radiation increases steadily up to certain frequency that is dependent on mouth radius and opening angle and decreases thereafter before increasing again depicting a periodic behavior.

Figure 12 shows the discrete digital filter approximation (dashed curve) to the radiation resistance computed analytically (solid curve) for the four gape half-angles. All curves are for a 0.5 cm mouth radius. Note that the effect of greater angle (smaller head size) produces a modest peak in the resistance prior to the drop to the high-frequency asymptote of 39.9 g/(cm² s).

Figure 13 shows the same set of curves for the 3.0 cm mouth radius. The only difference is the frequency-lowering of the peak and subsequent drop in resistance.

Figure 14 shows the high-frequency digital filter approximations (dashed curves) of the inductance for four angles and a mouth radius of 0.5 cm. The approximations are excellent over the entire span of frequencies.

Figure 15 shows the digital filter approximations of radiation inductance for a 3.0 cm mouth radius. The most important observation is the vertical scale change by a factor of 6. In addition, the two peaks have been lowered in frequency by a factor of about 6. These two factors produce a high radiation efficiency.

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