

Model for vocalization by a bird with distensible vocal cavity and open beak

Neville H. Fletcher^{a)}

Research School of Physical Sciences and Engineering, Australian National University,
Canberra 0200, Australia

Tobias Riede and Roderick A. Suthers

School of Medicine, Jordan Hall, Indiana University, Bloomington, Indiana 47405

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Some birds make use of a distensible oral cavity to produce nearly pure-tone song. Songbirds such as the Northern cardinal (*Cardinalis cardinalis*) have a muscularly distended oropharyngeal-esophageal cavity between the top of the trachea and the open beak. The present paper analyzes the acoustics of this vocal system. It is shown that the resonance of the oropharyngeal-esophageal cavity, vented through the beak, introduces a dominant peak in the radiation efficiency, the frequency of which can be adjusted by varying the volume of the cavity, the beak gape, and perhaps the position of the tongue in the mouth. To produce nearly pure-tone song, the bird adjusts the frequency of this peak to coincide with the fundamental of the syringeal oscillation. The present paper provides the acoustical analysis underlying this behavior. © 2006 Acoustical Society of America. [DOI: 10.1121/1.2159434]

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I. PURE-TONE BIRDSONG

While much birdsong consists of complex sounds with harmonic partials generated by air flow through the vibrating syringeal valve and a formant envelope imposed by resonances of the upper vocal tract, some birds are able to produce almost pure-tone songs. There has been speculation in the past that these songs might be produced by a completely different aerodynamic whistle mechanism, but experiments have now demonstrated that, at least in many cases, the syrinx is vibrating normally, though perhaps remaining partially open through its whole vibration cycle instead of closing for a part of it (Larsen and Goller, 1999). While this nonclosing valve oscillation certainly reduces the content of higher harmonics in the syringeal flow, some sort of narrow band-pass filter mechanism is required in the upper vocal tract to produce the single-tone calls with greatly attenuated upper harmonic content actually observed.

In the case of Ring doves (*Streptopelia risorea*), the mechanism involves an inflated esophagus and a closed beak. The upper esophagus is inflated to rather large volume so that its walls are very thin. The air flow from the syrinx is lightly filtered by the first resonance of the trachea, which may be adjusted by partial closure of the glottis, and then led into the inflated esophagus, the beak remaining closed during vocalization (Beckers *et al.*, 2003; Riede *et al.*, 2004). The air enclosed in the inflated esophagus, coupled to the vibrational motion of the sac walls, constitutes the necessary narrow-band filter, and sound is radiated directly by the wall vibrations (Fletcher *et al.*, 2004). The analysis indicates that the filter frequency is not very sensitive to esophagus infla-

tion provided it is moderately inflated, so that its tuning is not significantly altered during the rather brief duration of the “coo” song. This means, however, that the bird is not able to change its song pitch by an appreciable amount, and it remains close to the inflated sac resonance at about 600 Hz in the Ring doves studied.

Songbirds, however, such as the Northern cardinal (*Cardinalis cardinalis*), possess an actively distended oropharyngeal-esophageal cavity (hereafter referred to as the OEC) in the vocal tract, do not close their beaks during song, and are able to produce pure tones that can be swept rapidly over a wide range of frequency, even from 1 to 9 kHz, as described by Riede *et al.* (2006) in a companion experimental paper and illustrated in the penultimate figure of the present paper. For these birds, most of the OEC is embedded in tissue so that its walls do not vibrate much, and the song is then essentially that radiated through the beak. The present paper analyzes the acoustic performance of such a vocal system, examines the extent to which any OEC resonance is dominant over tracheal resonances, and explores the degree to which the OEC resonance can be modified by such variations in the anatomical parameters as could be made by the bird during song.

II. MODEL DESCRIPTION

The aim of this model is to present the basic features of the vocal tract of the bird in such a way that a calculation of its acoustic performance is possible without the intervention of too many unknown anatomical parameters. The dimensions of the trachea and other anatomical features are known from x-ray images of spontaneously singing birds and from anatomical dissections. The only adjustable parameters are taken to be the (a) constriction of the glottis, (b) the volume of the OEC, and (c) the acoustic loading produced by the

^{a)}Author to whom correspondence should be addressed. Electronic mail: neville.fletcher@anu.edu.au

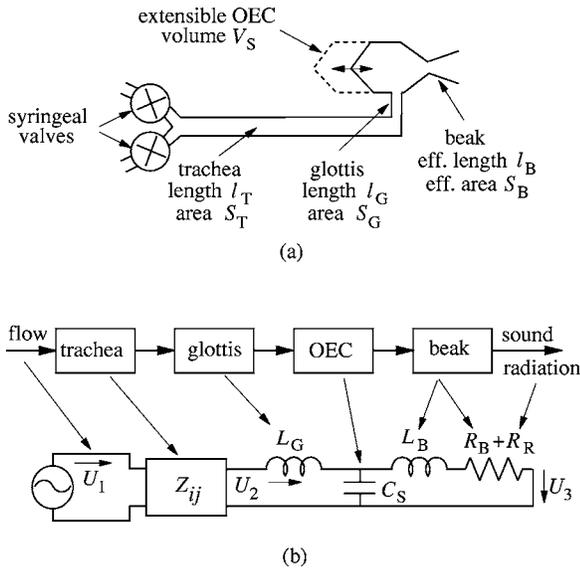


FIG. 1. (a) Sketch of the vocal system of the bird that is studied. Symbols define the dimensions used in the model. (b) Elements of the acoustic system describing the bird vocal system in (a), together with the electrical network analog circuit used in the calculation.

mouth and beak, reduced to a single parameter related to beak gape. Since in the cardinal the syrinx is very close to the tracheal bifurcation, resonances of the bronchi below the bifurcation, which were considered in an earlier birdsong model (Fletcher and Tarnopolsky, 1999), can be neglected. It is then assumed that the active syringeal valve behaves as a high-impedance acoustic source injecting a constant volume flow amplitude at frequency $f = \omega/2\pi$ into the base of the trachea.

The physical model for the vocal system is shown in Fig. 1(a), the acoustic model in the upper part of Fig. 1(b), and the electric analog network computational model in the lower part of Fig. 1(b). The meanings of the symbols are defined in the diagram and will be discussed in what follows. An electric network analog model is used since this is common in acoustics and makes the calculation simple. In this model, acoustic pressure is represented by electric potential and acoustic volume flow by electric current (Fletcher, 1992). The electrical analogs of short constrictions then ap-

pear as inductors (L) and cavities that are a good deal smaller than the wavelength as capacitors (C), while tubes are four-terminal impedance elements Z_{ij} .

A much more detailed model of the vocal anatomy could easily be formulated, recognizing in particular that the OEC is a tubelike structure with the mouth at one end and the glottis entering about half-way along one side. Such a model might also take into account the detailed taper of the OEC at the mouth end. To do all this, however, would add a great deal more complication to the analysis and require several extra parameters and would make little difference to the calculated results for frequencies less than that at which the OEC is half a wavelength long. This complication becomes significant at frequencies above about 6 kHz for a fully distended OEC and above about 12 kHz when it is collapsed. In view of the approximations made in other aspects of the analysis, this complication has not been included, but the frequency limitations of the simple model are shown when the results are displayed.

Using the symbols as defined in Fig. 1, the network equations can be simply solved to show that the acoustic flow U_3 through the beak at frequency ω for an input flow U_1 is given by

$$U_3 = \frac{-jZ_{12}\omega C_S U_1}{1 - (1 - \omega^2 L_B C_S + j\omega R_B C_S)(1 - \omega^2 L_G C_S + j\omega C_S Z_{22})}, \quad (1)$$

where $j = \sqrt{-1}$ as usual, and the impedances still have to be defined in terms of the physical dimensions of the system. The necessary results are as follows, defined in each case in terms of the dimensions shown in Fig. 1(a) (Fletcher, 1992):

$$Z_{11} = Z_{22} = -jZ_0 \cot kl_T, \quad (2)$$

$$Z_{21} = Z_{12} = -jZ_0 \operatorname{cosec} kl_T, \quad (3)$$

where $Z_0 = \rho c / S_T$ with ρ the density of air and c the speed of sound in air, and $k = \omega/c - j\alpha$ where the attenuation coefficient α is given by $\alpha \approx 10^{-5} \beta \omega^{1/2} a^{-1}$ with a being the effective radius of the trachea, given by $S_T = \pi a^2$, and β is an extra loss coefficient ($1 < \beta < 10$) for the walls of the trachea (Fletcher, 1992). When the complex nature of k is included specifically, it follows that

$$Z_{11} = Z_{22} = -Z_0 \frac{\sinh(\alpha l_T) \cosh(\alpha l_T) + j \sin(\omega l_T / c) \cos(\omega l_T / c)}{[\sin(\omega l_T / c) \cosh(\alpha l_T)]^2 + [\cos(\omega l_T / c) \sinh(\alpha l_T)]^2}, \quad (4)$$

$$Z_{21} = Z_{12} = -Z_0 \frac{\cos(\omega l_T / c) \sinh(\alpha l_T) + j \sin(\omega l_T / c) \cosh(\alpha l_T)}{[\sin(\omega l_T / c) \cosh(\alpha l_T)]^2 + [\cos(\omega l_T / c) \sinh(\alpha l_T)]^2}. \quad (5)$$

The glottal constriction, assumed to have effective length l_G and area S_G , has an analog inductance $L_G = \rho l_G / S_G$. It should be noted that, since the length of the distended OEC is not always small compared with the sound wavelength, a really careful model would include the possi-

bility of internal resonances within the OEC itself. These are difficult to model, since the OEC does not have a simple shape, but a first-order model in which it is treated as a simple cylinder with the glottis near the mid-point is outlined in the Appendix. Calculations using this model show that

there is, as expected, a sharp minimum in the output from the beak when the OEC length is exactly half the sound wavelength. Above this frequency there is an additional series of maxima when the OEC length is an odd number of quarter wavelengths of the sound. This model is not pursued in detail, since it is not anatomically accurate, but its findings indicate that the results of the present calculation are not accurate at high frequencies for a greatly extended OEC and, for this reason, the calculated results to be shown later are all truncated at the frequency above which they become unreliable.

Possible vibration of the walls of the OEC contributes an effective inductance $L_W \approx \rho_W T_W / A_W^2$, where ρ_W is the mass density of the tissue surrounding the cavity, T_W is the thickness of this tissue, and A_W is the total area of the cavity walls. An important anatomical distinction between the cardinal and the dove is that the OEC is embedded in other tissue, giving a large value of T_W , while the expanded esophagus of the dove is essentially exposed when inflated. This wall inductance L_W is in parallel with the impedance of the air passage through the beak. However, its magnitude is so much greater than that of the beak vent that it can validly be neglected. Any wall vibration will also contribute an additional loss to the system but, in the absence of any data, this is neglected.

The beak is much more complicated, since its impedance depends upon the nature of the constriction at its junction with the OEC, the position of the tongue and the extent to which this constricts the passage through the mouth into the beak, and the dimensions and opening angle of the beak itself. It is well known that the mouth geometry is crucial in determining the frequencies of the formant resonances in human speech, and the same has been found to be true of parrots (Patterson and Pepperberg, 1994; Beckers *et al.*, 2004). As discussed in detail elsewhere (Fletcher and Tarnopolsky, 1999) and verified by experiment for a simplified beak geometry, the beak contributes an inertive (i.e., inductive) load to the OEC opening. For a typical conical beak about five times as long as its base diameter, the result is that the beak behaves as an open tube equal to its base in diameter and with an effective length l_{eff} that varies between about half its geometrical length when it is nearly closed down to about one-tenth of this length when its tip is opened to more than about one-third of the beak length. This acoustic length also depends upon frequency f , and a regression to fit the experimental results has the form

$$l_{\text{eff}} \approx 0.05l_B + 0.03 \frac{l_B^2}{g\lambda} \approx 0.05l_B + 10^{-4} \frac{f l_B^3}{g}, \quad (6)$$

where g is the tip opening and λ is the sound wavelength. The second form of writing assumes that dimensions are given in meters. This expression, which is reasonably accurate for $g < l_B$, that is for a gape angle of less than about 60° , and for a frequency f such that $f < 500/l_B$, is illustrated in Fig. 2. [Note that the expression (6) has been modified slightly from that in the original paper by insertion of an extra factor $10/l_B$ to scale the frequency properly with beak length.] If the root diameter of the beak is d_B , then its acoustic inertance is about

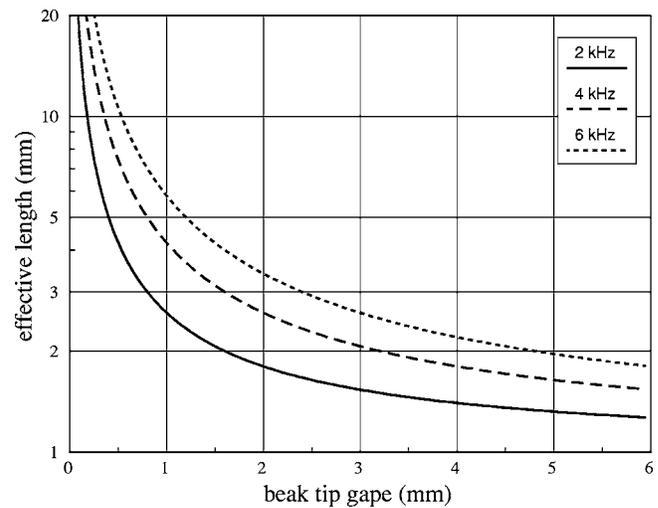


FIG. 2. Plot of the relation (6) giving the effective acoustic length as a function of frequency f and tip gape g , for the case of a beak 20 mm in length and 4 mm in effective diameter at its base.

$$L_B \approx \frac{4l_{\text{eff}}}{\pi d_B^2}. \quad (7)$$

It can be seen from Fig. 2 that the effective acoustic length of the beak is very small unless it is almost closed and saturates to a value of a little more than 1 mm for a widely open beak, this being largely due to the radiation impedance. This figure is not strictly applicable to the beak of the cardinal, since here the root diameter is more like one-fifth of the beak length, and the actual tip gape during singing ranges from nearly 0 to about 4 mm, but the general behavior will be very similar. This leads to the conclusion that beak opening is not the controlling factor influencing the dominant frequency of the song syllable, but rather a combination of the OEC volume and the beak gape.

There may be an additional inertive load contributed by the constriction caused by the tongue, depending upon how this is raised during song, which may well be correlated with the beak gape. For simplicity, however, this will be simply included with the beak inertance as defined by its effective length and root diameter. This is accomplished by defining a parameter G , which will in what follows be called the gape parameter, through the relation

$$L_B = \frac{\rho l_B}{S_B} = \frac{\rho}{G}. \quad (8)$$

This parameter G is then measured in meters (or more conveniently in millimeters) and increases as the beak is opened or the tongue lowered so as to reduce its constricting effect. Reasonable anatomical considerations suggest that, for the birds considered, G lies in the range 1–7 mm. The value of G is positively correlated with, but not numerically equal to, the physical opening of the beak tip.

This gape parameter G will be used in the illustrative calculations in the next section. Note that, even if the mouth and beak were so widely open that each could be assumed to have zero length for a trial calculation, G could still not exceed about 10 mm because of the inertive component of

the radiation impedance of a simple opening, which is equivalent to that of a tube matching this opening and about 0.3 times its diameter in length (Fletcher, 1992). Most of the acoustic tuning effect of the beak and mouth thus occur when the beak is nearly closed, in agreement with the findings of Nelson *et al.* (2004). From the curves of Fig. 2, the parameter G , while positively correlated with actual beak gape, does not vary linearly with this quantity, most of the variation in G occurring when the beak is nearly closed. In addition, from (8) the variation in G could be largely caused by variation in the root area S_B of the beak or by variation in the shape of the OEC where it joins the beak, which is included in this parameter. Care should therefore be taken when interpreting the parameter G in the results to be displayed later.

The acoustic impedance of the mouth and beak, as calculated above, is simply the inertive component, and to this must be added a resistance $R_B \ll Z_0$, where $Z_0 = \rho c / S_T$ is the characteristic impedance of the trachea. This resistance is due largely to viscous losses in the various constrictions around the tongue and the sharp edges of the beak, since the radiation resistance is negligibly small in comparison. Quantification of this resistance is difficult since it depends upon things such as the sharpness of the edges of the beak and the shape and roughness of the tongue. It must therefore be regarded as a rather poorly specified adjustable parameter, but its value simply affects the sharpness of some of the resonance peaks. Finally, there is the radiation resistance R_R , as shown in Fig. 1. Since $R_R \ll R_B$, it can however be neglected for the purposes of the network analysis.

With these definitions, the analysis is complete, though the expressions for the impedance coefficients Z_{ij} must be expanded to take account of the complex nature of k as indicated in (4) and (5), and Eq. (1) must then be simplified to give the magnitude $|U_3|$ of the acoustic flow from the beak. Since the equivalent cross-section diameter of the beak aperture is generally small compared with the sound wavelength, the acoustic radiation resistance R_R varies approximately as ω^2 so that the radiated acoustic power at frequency ω is proportional to $\omega^2 U_3^2$ (Fletcher, 1992). Expressed as usual in decibels relative to some arbitrary reference, the sound level is given by $20 \log_{10}(\omega U_3) + \text{const}$. In the calculations to follow it will be assumed that the magnitude of U_1 is independent of frequency so that a spectral response function can be calculated. For an actual bird call, the syringeal mechanics will determine the relative amplitudes of the harmonics of the fundamental in the syringeal flow (Fletcher, 1988) and, from this and the response function derived above, the spectrum of the radiated song can be calculated.

III. RESULTS AND CONCLUSIONS

It is straightforward to implement a computer program to calculate the relative radiated power level $20 \log_{10}(\omega U_3)$ as a function of frequency for particular values of the parameters that the bird varies during song, namely the OEC volume V_S , the beak gape parameter G , and perhaps the glottal constriction S_G , and for reasonable assumed values for the other parameters. For the particular case studied here, the Northern cardinal, these parameters are shown in Table I.

TABLE I. Assumed parameter values.

length of trachea	l_T	48 mm
diameter of trachea	d_T	1.6 mm
loss factor of trachea	β	3
length of glottis	L_G	2 mm
diameter of glottis	d_G	1 mm
length of OEC	l_S	5–20 mm
volume of OEC	V_S	0.3–2 ml
loss resistance of beak	R_B	10^5 Pa s m^{-3}

Figures 3 and 4 show the calculated acoustic power output for a constant glottal flow at a given frequency. As is most clearly shown in Fig. 3, there are four acoustic resonant reinforcement peaks. The frequencies of the peaks at about 1.2, 4, and 7 kHz, indicated by arrows, are associated with tracheal resonances and vary rather little with changes in the gape parameter G , while the frequency of the most promi-

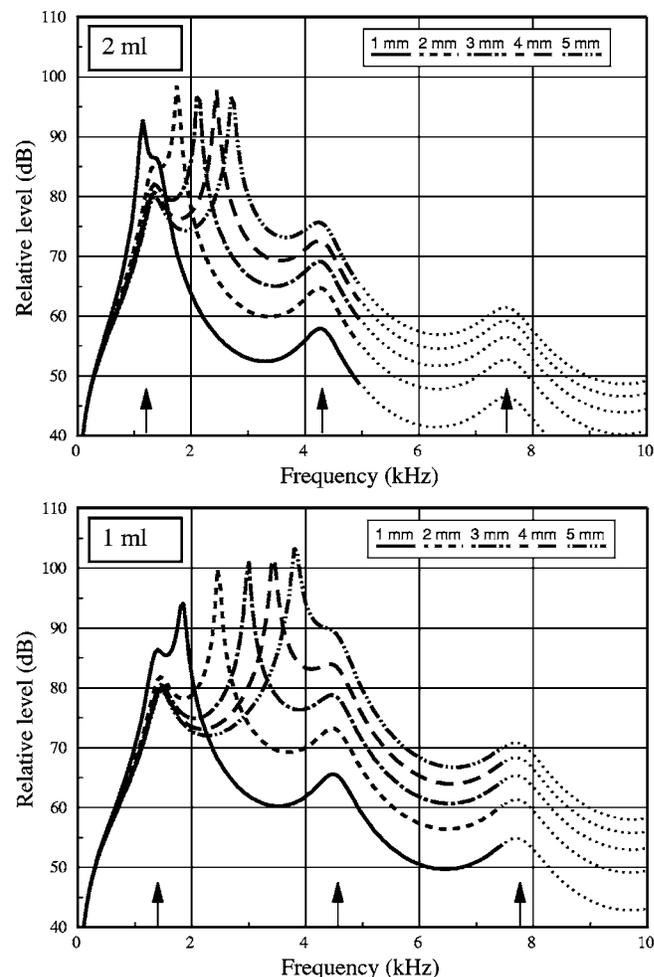


FIG. 3. Relative radiated power level as a function of frequency, for a constant input volume flow at the syrinx, with a OEC volume of 2 or 1 ml and various values of the gape parameter G . Other parameters are as shown in Table I. The location of the variable OEC resonance peak is shown to depend upon both beak gape and OEC volume, while the frequencies of the three tracheal resonances, near 1.5, 4.5, and 7.5 kHz and indicated by arrows, are little affected by these parameters unless there is a near coincidence with the OEC peak. The predictions of the model are not accurate above frequencies for which the wavelength is less than about twice the OEC length, and the curves are shown dotted in this region.

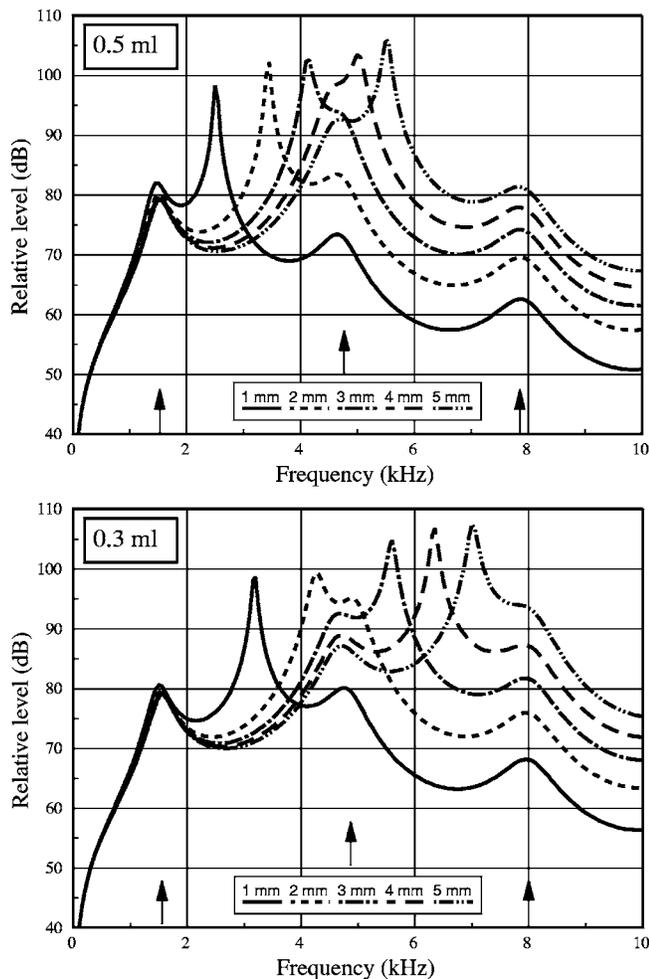


FIG. 4. Plots similar to those of Fig. 3 for OEC volumes of 0.5 or 0.3 ml as functions of beak gap parameter G . Other comments are as for Fig. 3.

ment resonance in the range 1–4 kHz, in contrast, depends strongly on G , as well as on the OEC volume V_S . Figure 4 shows the results of similar calculations with two smaller assumed OEC volumes, allowing the dominant resonance to be moved as high as 7 kHz. Note that, when the frequency of this variable resonance approaches that of one of the tracheal resonance peaks, as shown most clearly in Fig. 4(a) for $G = 3$ mm and in Fig. 4(b) for $G = 2$ mm, there is an acoustic interaction and, over a small parameter range, the heights of the two peaks are nearly equal before the dominant resonance frequency jumps from one to the other.

The relative prominence of the tracheal peaks depends upon the wall losses in the trachea, the value assumed in the calculation being that for a moderately smooth tube of uniform diameter. In addition to this, however, since the OEC acts to some extent as a low-pass filter, its presence reduces the prominence of all tracheal resonances above the frequency of the OEC resonance. This effect is greatest when the OEC volume is large, as is readily seen by comparing Figs. 3 and 4. The prominence of the variable OEC resonance peak depends mostly upon the assumed value of the resistive losses in the mouth and beak. Using the assumed parameter values, however, the dominant resonance peak is always that associated with the OEC. The frequency of this peak as a function of the gape parameter G is shown in Fig.

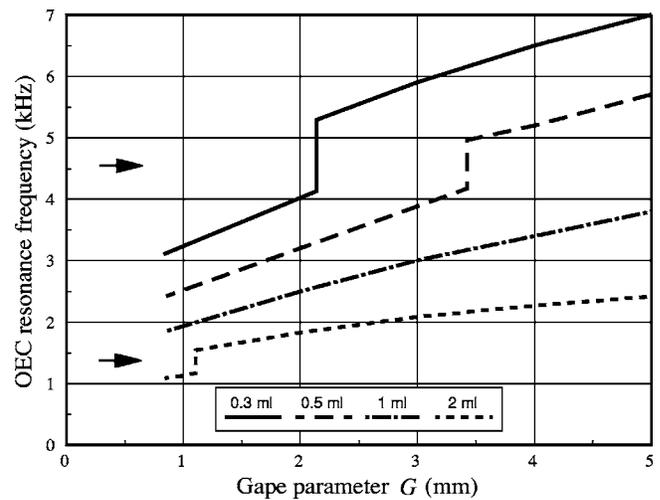


FIG. 5. Frequency of the dominant resonance peak of the vocal tract as a function of beak gape parameter G for four different OEC volumes. The tracheal resonances are at about 1.5 and 4.5 kHz, as indicated by the arrows. The curves do not reach the 7.5-kHz resonance.

5, for the four OEC volumes used in the calculation. The sudden jumps in frequency occur when the dominant resonance passes through the frequency of one of the tracheal resonances. It is clear that, by varying the mouth configuration, beak opening, and OEC volume over the reasonable ranges assumed, the bird can tune the prominent vocal tract resonance over a wide range from below 1 kHz to about 7 kHz. At some frequencies there may be two or more combinations of OEC volume and beak gape that provide the necessary resonance frequency. For example, referring to Fig. 5, an OEC resonance and thus a song frequency match at 3.5 kHz could be achieved with an OEC volume of 0.3 ml and a beak gape parameter of 1.5 mm, with an OEC volume of 0.5 ml and a gape of 2.5 mm, or an OEC volume of 1 ml and a gape of 4.5 mm. The bird is able to choose whichever of these options, or others in between, is most convenient for the syllable being sung.

The bird will presumably match the vibration frequency of its active syringeal valve with that of this variable resonance, thus ensuring a large vocal output at this fundamental frequency, which can be varied over at least the range 1–7 kHz. It is reasonable that the two syringeal valves may differ slightly in thickness and musculature so that one is used for the lower and one for the higher notes.

Because the air flow through the syringeal valve is nonlinear, this generates all harmonics of the fundamental frequency in the flow U_1 , as has been discussed elsewhere (Fletcher, 1988), the harmonic amplitudes generally decreasing smoothly in amplitude with increasing frequency at about 6 dB/oct (i.e., as ω^{-1}). On top of this, the properties of the vocal OEC lead to a deemphasis of frequencies above the OEC resonance, as is particularly noticeable in Fig. 3. Since there are no higher resonances of the OEC to consider, and since it is unlikely that any of the subsidiary tracheal resonances will happen to coincide with upper harmonics of the excitation frequency, these upper harmonics of the syringeal flow will be very weak in the radiated spectrum, and the song will have a predominantly pure-tone nature. Exami-

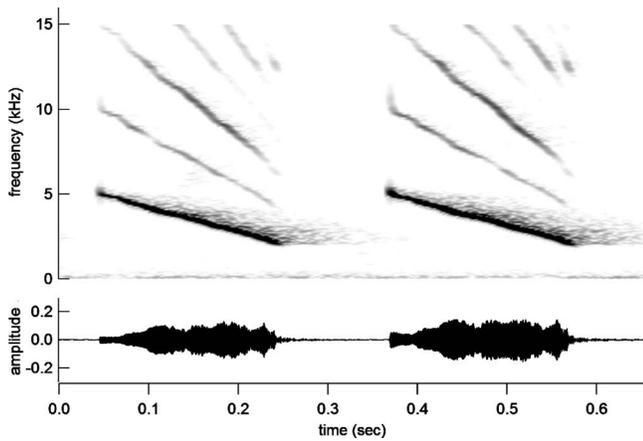


FIG. 6. Waveform and time-resolved spectrum of two syllables sung by a cardinal. The dominant fundamental is associated with the adjustable resonance of the OEC, while the two broad formant bands at about 7, 10, and 14 kHz appear to be associated with the fixed tracheal resonances revealed by the analysis.

nation of Figs. 3 and 4 shows that the peak associated with the OEC resonance is 10–15 dB higher than the nearest tracheal resonance peak. This implies a corresponding advantage in the power radiated at this frequency and explains why evolution may have favored this development.

Additional supporting data for the model are shown in Fig. 6, which gives the waveforms and time-resolved spectra for two downward sweeping syllables of the cardinal’s song. There is clearly one dominant frequency component of the sweep, decreasing in frequency from about 6 to 3 kHz, which we identify with the major resonance of the OEC, as discussed above. In addition, however, there are emphasized formant bands in the much weaker higher harmonics of this fundamental, centered round 7, 10, and 14 kHz, which might reasonably be taken to be associated with the fixed tracheal resonances identified in the analysis. The lack of quantitative agreement between these frequencies and those calculated is not very significant, since the model is primarily concerned with the major OEC resonance and its accuracy declines at high frequencies.

One apparent problem of a behavioral nature is the necessity for the bird to adjust the frequency of its syringeal vibration to match that of the major OEC resonance. While it is true that immature birds do find difficulty in producing substantially pure-tone songs, perhaps for this very reason, it does appear to be a rather difficult task. Fortunately there is a simple solution to this apparent dilemma. In all the discussion above it has been assumed that the bird produces a complex harmonic acoustic flow through the syringeal valve and that this signal is then simply filtered by the vocal tract, a model known as the “source-filter approximation.” While this is a good approximation in the case of birds such as the raven (Fletcher, 1988), since the frequency of the fundamental is much less than that of the first vocal tract resonance, this is no longer true for the birds under consideration here. Instead, when the frequency of a major vocal tract resonance is close to that of the vibrating valve source, there is a major feedback interaction that tends to shift the frequency of the valve oscillation into close match with that of the resonance

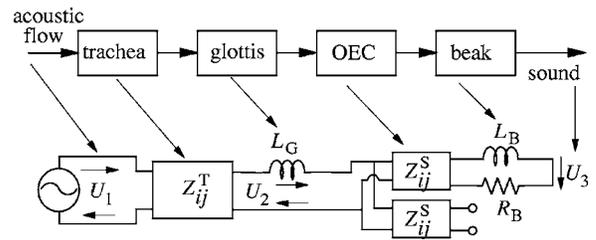


FIG. 7. The acoustic system showing the OEC as a cylinder with the glottal entry at its mid-point, together with the electrical network used to model the behavior of this system.

(Fletcher, 1978). The reason for this is that the valve oscillation is driven by the pressure difference across it, and this is strongly influenced on the downstream side by vocal tract resonances. What this implies, therefore, is that the major tuning action is that of distension of the OEC coupled to beak gape, and that, provided the vibrational frequency of the syringeal valve is adjusted to approximate agreement, the coupling mechanism will lock its frequency to that of the resonance. In this connection, “approximate agreement” means to within about $\pm f_s/Q$ where f_s is the OEC resonance frequency and Q is the quality factor of the undriven valve, which is probably less than 10 because of losses when the valve closes. The required frequency match accuracy is probably thus not as strict as $\pm 10\%$.

It should perhaps be emphasized once again that the model presented here has used the simplest anatomical approximations possible in order to present the fundamentals of the operation of the vocal system of birds such as the cardinal. Many refinements could be introduced, at the expense of introducing additional parameters, but should not affect the overall predictions in the frequency ranges shown.

APPENDIX: EXTENDED TREATMENT

The physical model for the vocal system shown in Fig. 1(a) can be refined by treating the OEC as an extended object with the trachea entering at the glottis half way along its length. The acoustic model for this system is shown in the upper part of Fig. 7, and the electric analog network computational model in the lower part of Fig. 7. Because the OEC, when fully distended, is nearly 30 mm in length, it is necessary to represent it by a pair of four-terminal impedances with the flow from the glottis entering between them. One of these elements leads to the beak, while the other is terminated by a closed wall with only a very small hole leading to the non-distended part of the esophagus, so that there is essentially no acoustic flow at its remote end, which is therefore shown as an open circuit.

Using the symbols as defined in Fig. 1 but with Z_{ij}^T representing the impedance coefficients for the trachea and Z_{ij}^S , those for the half-length of the OEC, the network equations can be solved to show that the acoustic flow U_3 through the beak at frequency ω for an input flow U_1 is given by

$$U_3 = \frac{Z_{11}^S Z_{12}^S Z_{12}^T}{[Z_{11}^S + 2Z_{11}^T + 2Z_G][Z_{11}^S Z_B + (Z_{11}^S)^2] - (Z_{12}^S)^2 (Z_{11}^S + Z_{11}^R + Z_G)}, \quad (\text{A1})$$

where the impedances still have to be defined in terms of the physical dimensions of the system.

This system cannot be modeled until the physical dimensions of the OEC have been fully specified, and this is difficult since they vary smoothly with OEC distention. As a representative case, the OEC can be treated as a simple cylinder so that the coefficients Z_{ij}^S have the same form as those given in (4) and (5) for the trachea, with appropriate dimensional changes. Implementation of the model then shows that it gives results that are essentially identical with those of the simple cavity model discussed in the main text for frequencies such that the total OEC length is less than about 0.4 times the sound wavelength. Above this frequency there are additional maxima and minima in the response. This model is not pursued in detail, since it is not anatomically realistic. A more realistic model could, however, be constructed using the result (A1) and values of the impedance coefficients Z_{ij}^S appropriate to the actual OEC geometry if this were known in detail. The actual calculation of these coefficients would, however, be quite complicated.

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