

Vocal tract filtering and the ‘coo’ of doves

Neville H. Fletcher*

*Research School of Physical Sciences and Engineering,
Australian National University, Canberra 0200, Australia[†]*

Tobias Riede

*Institute for Theoretical Biology, Humboldt-University Berlin,
Invalidenstrasse 43, 10115 Berlin, Germany*

Gabriël J.L. Beckers

*Behavioural Biology, Institute of Biology, Leiden University,
PO Box 9516, 2300 RA Leiden, Netherlands*

Roderick A. Suthers

*School of Medicine,
Jordan Hall, Indiana University,
Bloomington, IN 47405, USA*

(Dated: March 11, 2004)

* corresponding author

[†]Electronic address: neville.fletcher@anu.edu.au

ABSTRACT

Ring doves (*Streptopelia risoria*) produce a ‘coo’ vocalization that is essentially a pure-tone sound at a frequency of about 600 Hz and with a duration of about 1.5 s. While making this vocalization, the dove inflates the upper part of its esophagus to form a thin-walled sac structure that radiates sound to the surroundings. It is a reasonable assumption that the combined influence of the trachea, glottis and inflated upper esophagus acts as an effective band-pass filter to eliminate higher harmonics generated by the vibrating syringeal valve. Calculations reported here indicate that this is indeed the case. The tracheal tube, terminated by a glottal constriction, is the initial resonant structure, and subsequent resonant filtering takes place through the action of the inflated esophageal sac. The inflated esophagus proves to be a more efficient sound radiating mechanism than an open beak. The action of this sac is only moderately affected by the degree of inflation, although an uninflated esophagus is inactive as a sound radiator. These conclusions are supported by measurements and observations that have been reported in a companion paper.

PACS: 80Ka

I. INTRODUCTION

Birdsong has a wide variety of forms, as described in the classic book by Greenewalt (1968). Some birds produce melodically rich extended songs with individual notes that are almost pure-tone in some species but rich in harmonics in others. Other birds, such as crows, may produce simple vocalizations with harmonically rich spectra that are shaped into formant bands as in human speech. Some cockatoos even produce chaotic non-harmonic cries (Fletcher 2000). Surveys of the mechanisms involved in some of these cases have been given by Brackenbury (1982) and others, while quantitative models for some of these systems have been developed by Casey and Gaunt (1985), by Fletcher (1988) and by Fletcher and Tarnopolsky (1999). The case of Ring doves is rather different in that they often produce simple pure-tone coos in a relatively narrow frequency range, and do so with their upper esophagus inflated to a large sac that effectively radiates the sound while the beak remains closed. Apart from this feature, the vocal system of the dove differs little from that of other birds (Ballintijn et al. 1995). Extensive studies of doves have recently been published by Beckers et al. (2003a,b) and by Riede et al. (2004), and these provide the experimental basis of the present paper. These papers contain numerous references to the relevant literature and provide the experimental data upon which the present paper is based.

The prominence of the inflated esophagus (the abbreviation IE will be used henceforth) during song invites the conclusion that it is acoustically important, and this is the hypothesis that is explored here. It is possible, however, that it is simply a display feature used in courtship. The fact that the beak is closed during song leads to the tentative conclusion that the resonances of the mouth and beak that are so important in the song of some other birds are irrelevant in the case of the dove, but that leaves the length of trachea connecting the syrinx to the expanded esophagus as a possible contributor to resonance. The sound passes through the glottis at the entry to the trachea, so that constriction of this passageway may also contribute to overall behavior.

The purpose of the present paper is thus to examine the role of these anatomical structures in providing a very efficient filter for the generally harmonically rich sound that is expected to be generated by the vibrating syringeal valve. Since mere speculation and modeling is inadequate, the model will be tested by comparison with the experimental data on song in the Ring dove (*Streptopelia risoria*) provided by the study of Riede et al. (2004).

II. ACOUSTIC MODEL

X-ray photographs of a dove while singing are given by Riede et al. (2004), and from these it is possible to derive anatomical details. For the purpose of acoustic modeling, details such as the precise location and curvature of the trachea are unimportant, and the vocal system can be treated in terms of the simplified anatomy shown in Fig. 1. The anatomical dimensions, given by the data of Riede et al., are shown in Table 1.

Figure 2(a) shows an electric analog circuit that represents the acoustic system of Fig. 1. In such a circuit the analog of acoustic volume flow is electric current and the analog of acoustic pressure is electric potential (Fletcher 1992). The lungs provide a constant pressure (voltage) of about 1.5 kPa (15 cm water gauge) and the syrinx behaves like a valve oscillating at a frequency $f = \omega/2\pi$ of about 600 Hz. Since the lung pressure is high relative to that in the trachea, the impedance of the syringeal source is high, and it can be considered to inject a volume flow of constant amplitude. Because the valve almost closes once in each cycle, the acoustic volume flow into the base of the trachea is rich in harmonic overtones (Fletcher 1988).

It is interesting to note that, while the trachea and glottis constitute a series impedance, the components of the inflated esophageal sac constitute a parallel impedance. The interaction between these two impedances, themselves in series with one another, is a little complex and generally results in a pair of resonances, even if they are adjusted to the same resonance frequency. This need not be of concern, since it is automatically taken into account in the analysis.

A. Tracheal and glottal impedances

The tracheal tube is represented by a four-terminal element with impedance coefficients Z_{ij} given by (Kinsler et al. 1982, Fletcher 1992)

$$\begin{aligned} Z_{11} = Z_{22} &= -jZ_0 \cot kL \\ Z_{12} = Z_{21} &= -jZ_0 \operatorname{cosec} kL. \end{aligned} \tag{1}$$

Here L is the length of the trachea, $Z_0 = \rho c/S_T$ where $\rho \approx 1.2 \text{ kg/m}^3$ is the density and $c \approx 350 \text{ m/s}$ the velocity of sound in air at dove body temperature, $S = \pi d^2/4$ is the area

of the trachea, $k = (\omega/c) - j\alpha$ is the complex wave number for sound of angular frequency $\omega = 2\pi f$ and attenuation coefficient $\alpha \approx 2.4 \times 10^{-5} \omega^{1/2}/d$ in the tracheal tube of diameter d , and $j = \sqrt{-1}$. The acoustic pressures p_i and acoustic volume flows U_i at the two ends of the tube are then related by

$$p_i = \sum_j Z_{ij} U_j. \quad (2)$$

If the impedance connected to the upper end of the trachea is $Z_L = p_2/U_2$, then it follows from these equations that the input impedance Z_{in} at the syringeal end of the trachea is

$$\begin{aligned} Z_{\text{in}} &= \frac{p_1}{U_1} = \frac{Z_L Z_{11} - Z_{11} Z_{22} + Z_{12} Z_{21}}{Z_L - Z_{22}} \\ &= Z_0 \frac{Z_L \cos kL + j Z_0 \sin kL}{j Z_L \sin kL + Z_0 \cos kL}. \end{aligned} \quad (3)$$

Since the syrnix is a high-impedance source, it is tempting to simply select a frequency to maximize the real part of this input impedance, since maximum power will then be transferred to the vocal tract, but this does not give information about radiated acoustic power — the input power may be simply dissipated in viscous and thermal losses within the tract.

The glottal constriction to a narrow tube of length l and diameter g can be represented, since it is so short and narrow, by a simple inductive impedance in series with a resistive viscous loss (Fletcher 1992), giving an impedance

$$Z_G \approx \frac{4\rho c}{\pi g^2} \left(\frac{2.4 \times 10^{-5} l}{g} + j \frac{4\rho(l + 0.6g)\omega}{\pi g^2} \right), \quad (4)$$

where l is the length and g the diameter of the constriction. This is a valid approximation since the length of the glottal constriction is much less than the sound wavelength involved.

B. Impedance of the inflated esophagus

When an acoustic current flows into the inflated esophagus from the trachea it tends to both compress the contained air and also to expand the elastic containing wall. The acoustic impedances of these two elements are effectively in parallel, as shown in Fig. 2, since they both experience the same acoustic pressure but the acoustic flow is divided between them. The acoustic impedance of the air contained within the IE, neglecting the effect of the small overpressure created by wall tension, is

$$Z_V \approx -j \frac{\rho c^2}{V \omega} = -j \frac{\gamma p_0}{V \omega}, \quad (5)$$

where

$$V \approx \frac{4}{3}\pi a^2 b \quad (6)$$

is the volume of the IE, p_0 is the normal atmospheric pressure (100 kPa), and $\gamma = 1.4$ is the ratio of specific heats for air.

The walls of the IE, which expand and contract under the influence of the oscillating acoustic pressure within the IE and carry with them the overlying tissues and feathers, present an impedance that is the sum of an inertance due to the wall mass, a spring-like term due to the elasticity of the walls, and a resistive term due to viscous and other losses within the material of the wall. The radiation load on the outside of the walls is small enough to be neglected. This leads to an expression for the wall impedance of the form

$$Z_W \approx R + j \frac{m\omega}{S_W^2} + jX, \quad (7)$$

where m is the total mass of the walls,

$$S_W \approx 4\pi ab \quad (8)$$

is the total wall area, R takes account of losses in the walls, and the final term jX takes account of the elastic resilience of the walls, the form and magnitude of which will be discussed below. (Actually jX turns out to be negligible compared with the second term in the equation.) The total impedance presented by the IE to the trachea is then

$$Z_S = \frac{Z_W Z_V}{Z_W + Z_V}. \quad (9)$$

Exact calculation of the contribution of elasticity to the total wall impedance is complicated by the fact that the esophagus has expanded primarily in the radial direction a , while the length $2b$ has only increased a little. The skin tension is thus not isotropic but essentially concentrated in the plane normal to the length b of the esophagus. If the uninflated esophageal tube is taken to have radius a_0 and length b_0 , and the inflated sac to be approximately a prolate spheroid with short radius a and long radius $b \approx b_0$, then the surface area has expanded from about $2\pi a_0 b_0$ to about βab , where the factor β lies somewhere in the range $2\pi \leq \beta \leq 4\pi$ depending upon the ratio b/a , being smaller if $b > a$. As will be shown below, the exact value is not significant here. If K is the relevant elastic modulus of the wall material, multiplied by the wall thickness and adjusted for stretch, then the tension in the

wall is largely in the equatorial plane and has a value close to

$$T \approx K(a - a_0), \quad (10)$$

and the equilibrium internal pressure excess Δp created to balance this tension is approximately

$$\Delta p \approx \frac{T}{a} \approx \frac{K(a - a_0)}{a}. \quad (11)$$

Equivalently, we can write

$$K \approx \frac{a\Delta p}{a - a_0}. \quad (12)$$

The elastic force per unit area of wall for an expansion of amplitude δa at frequency ω is $K\delta a/a$ while the inertial force is about $m\omega^2\delta a/S$ or $m\omega^2\delta a/\beta ab$. The ratio of inertial to elastic force at frequency ω is thus about

$$\frac{4\pi b\Delta p}{m\omega^2} \left(\frac{a}{a - a_0} \right) \sim 10^{-5} \Delta p \left(\frac{a}{a - a_0} \right), \quad (13)$$

where the second expression assumes that the frequency is about 600 Hz and the total wall mass about 1 g. Since $a \approx 10a_0$, the final factor is close to unity, and the IE overpressure Δp is only a few hundred pascals (i.e. a few centimeters of water pressure). The elastic force is therefore only about 10^{-2} times the inertial force, and so the term jX in equation (7) can be neglected.

Evaluation of the resistive term R in (7) is difficult without experimental measurements. Most biological materials are rather lossy because of the liquid-filled cells of which they are composed, so that the quality factor, or Q value, of the IE resonance, given by

$$Q = \frac{2\pi f^* m}{R}, \quad (14)$$

where f^* is the resonance frequency, is likely to be only about 10 and perhaps even less. This implies that R is probably about one-tenth of the magnitude of the inertial term at 600 Hz. Since the magnitude of the IE-wall damping is unknown, the choice of $Q = 10$ is speculative. A check of the calculated results for lower values of Q shows, however, that the only significant change is a reduction in the radiated power. There is little change in the range of required glottal constriction, since this serves mainly to tune the tracheal resonance.

C. Effective mass of the IE wall

The other major parameter required for the model is an estimate of the mass m of the IE walls. In the absence of measurements, the following argument provides an approximate value.

From the X-ray photographs of the neck of a dove with inflated esophagus (Riede et al. 2004), it appears the diameter of the neck of the bird is about 15 mm, so that its cross-sectional area is about 2 cm^2 . Approximately half of this cross-section is occupied by the spine, the trachea, and the interior of the esophagus, so that the area of tissue available to cover the surface of the expanded esophagus is about 1 cm^2 , or equivalently about 1 g of tissue per centimeter length of neck. Since the neck is about 5 cm in length, this provides an upper limit of about 5 g for the mass of the membrane surrounding the IE. To adopt this value would, however, be a gross overestimate, since some of the tissue is muscles, sinews and blood vessels. A more conservative estimate of 1 to 2 g does, however, seem reasonable.

The simplified treatment leading to (7), however, is based upon the assumption that all parts of the IE walls vibrate equally, so that the expression for the acoustic impedance involves the simple factor m/S_W^2 , where S_W is the total area of the IE walls. Because, however, the IE is about the shape of a prolate spheroid with diameter ratio about 5:3, it is most likely that the walls near the equator are thinner and vibrate with greater amplitude than those near the upper and lower ends of the IE. Suppose, as an extreme case, that vibration was confined to an equatorial band of mass m' and area $S' = S_W/2$. To achieve the same acoustic impedance, since the vibrating area is halved, the vibrating mass must be reduced to one-quarter of the total original value, or to half of the mass originally spread over that area. Thus a total wall mass of 2 g, for example, would have the same acoustic effect as 4 g distributed evenly over a symmetrically vibrating sphere of the same surface area. In the calculations to follow, the mass will therefore be regarded as a parameter that can be adjusted to some degree but that must be kept within these reasonable anatomical limits.

These estimates have been confirmed by examination of a dove body that had been kept in a sealed bag in a refrigerator for about 12 months. Dissection of the neck and discarding of those tissues that are clearly not part of the inflatable esophagus left a residual mass of 1.14 g along a neck length of between 4 and 5 cm. This is probably an underestimate of

the real mass, however, partly because of slight drying of the tissues during storage, and partly because of loss of a few feathers during dissection. The value of 2 g adopted in the calculation is therefore supportable.

D. Effect of esophageal inflation

During the ‘coo’ vocalization the dove exhales air into the esophageal sac, further inflating it. It is important to know the effect of this inflation on the resonance frequency of the IE. The ‘coo’ of a single vocalization lasts for about 1.5 s and, during that time, the dove exhales about 10 cm³ of air into the IE. The resonance frequency of the IE is given approximately by

$$\omega^* \approx \left(\frac{\gamma p_0 S^2}{Vm} \right)^{1/2}. \quad (15)$$

Since $V \propto a^2 b$ and $S \propto ab$, this indicates that $\omega^* \propto b^{1/2}$. But the length b of the IE is nearly constant and only the radius a increases with inflation, so that the resonance frequency ω^* is nearly independent of further inflation.

Even in the case of a IE expanding uniformly in all directions, the resonance frequency varies only as $b^{1/2}$ or $V^{1/6}$. The initial IE volume is about 30 cm³ and this could be expanded to about 40 cm³ during the coo, an increase of about 30%. This would lead to an increase of only about 5% in the resonance frequency, and this, it should be stressed, is an upper limit to the real situation. A realistic interpolation is to assume that the longitudinal axis bends slightly, since it is constrained on one side by the bird’s neck, and to take

$$b = b_0 \left(1 + \epsilon \frac{a^2}{b_0^2} \right), \quad (16)$$

where b_0 is the uninflated sac length and the numerical coefficient $\epsilon \leq 0.6$ gives an indication of the extent to which sac expansion occurs in the lengthwise b -direction for a given lateral expansion in the a -direction. A choice of $\epsilon = 0.1$ seems a reasonable estimate from the appearance of X-ray images of the singing bird, and will be used in a later evaluation. The frequency shift in this case will be intermediate between the ‘no-shift’ result if b is constant and the small shift that would be the result of uniform expansion.

The effect of complete deflation of the IE so that a is reduced to about 1.5 mm is, however, quite a different matter. As will be seen in a later calculation, such deflation

increases the effective impedance of the IE by several orders of magnitude and effectively prevents significant sound radiation.

III. PERFORMANCE CALCULATION

Because the syrinx is fed from the relatively high over-pressure in the bird's lungs, it injects an oscillating volume flow into the trachea, the magnitude of which depends very little upon the acoustic impedance presented by the trachea and associated structures. At the other end of the system, the acoustic power P radiated in the 'coo' sound is

$$P = CU_S^2\omega^2 \quad (17)$$

where C is a constant. This power is thus proportional to the square of the amplitude of the acoustic current passing through the extreme right branch of the analog circuit in Fig. 2(b), multiplied by the square of the frequency. This simplification is appropriate since the IE diameter is small compared with the wavelength of sound at the frequencies considered, so that it can be treated as a "simple source" (Morse 1948, Fletcher 1992 ch. 7).

From a standard analysis of the analog circuit in Fig. 2(b), and writing each impedance Z_i as $R_i + jX_i$, it can be readily shown that the acoustic current U_S through the impedance Z_S representing the IE walls when a current U is injected at the syrinx is given by

$$U_S^2 = \left[\frac{(X_{12}X_V)^2 + (R_{12}X_V)^2}{A^2 + B^2} \right] U^2 \quad (18)$$

where

$$\begin{aligned} A &= R_S(R_{22} + R_G) - (X_S + X_V)(X_{22} + X_G) - X_VX_S \\ B &= R_S(X_{22} + X_G) + (X_S + X_V)(R_{22} + R_G) + X_VR_S. \end{aligned} \quad (19)$$

Since the only readily adjustable parameter from the viewpoint of the bird is the diameter of the glottal constriction, the full curve in Fig. 3 shows an analysis of the effect that this has on output power, assuming a 'coo' frequency of 600 Hz, and with all the other parameters having the values given in Table I. It is clear that the power output depends critically upon this vocal adjustment. The full curve in Fig. 4 shows the relative power output as a function of frequency, assuming that the glottal constriction has been optimized in this way. It seems clear that the dove must learn to constrict the glottis in just this manner in order to be able to produce a 'coo' sound with reasonable power.

Figure 4 also has another implication. The syrinx is a nonlinear flow regulator and produces not only a flow at its fundamental oscillation frequency, but also ‘harmonic’ components at frequencies that are precise integer multiples of that frequency. The flow amplitudes associated with these harmonics are less than that of the fundamental, but still not negligible. A pressure sensing microphone placed in the trachea will therefore detect these harmonics, as has been established by Riede et al. (2004). The calculation leading to Fig. 4 shows, however, that the efficiency with which these harmonics influence the motion of the skin of the IE is vanishingly small, so that they do not show up in the radiated sound. The IE effectively acts as an acoustic band-pass filter tuned to the song frequency near 600 Hz.

Since the full curves in Figs 3 and 4 were calculated on the basis of a IE resonance that is close to the coo frequency of 600 Hz, it is interesting to see what happens if the IE resonance is adjusted away from this frequency. The broken curves in Figs 3 and 4 are calculated with the vibrating mass of the IE wall reduced by a factor 2 to 1 g, so that its resonance frequency is raised by a factor $2^{1/2} \approx 1.4$. The output power at 600 Hz is greatly reduced even with an optimized glottal constriction, as shown in Fig. 3, though there is a minor peak at about 900 Hz in Fig. 4. The coo frequency could, of course, be adjusted to 900 Hz and a related adjustment made to the glottal constriction to take advantage of this resonance, but it would then be the call of a different bird.

Fig. 5 examines the effect of IE inflation upon radiated sound. The full curve is calculated on the assumption that the longitudinal inflation coefficient ϵ of (16) has the value 0.1, which appears to be a reasonable approximation to the real situation. There is a broad peak in the output near the actual IE diameter value $2a = 35$ mm. More importantly, however, the curve shows that the output declines almost to zero when the IE is deflated, agreeing with experimental observations. Since the exact value of ϵ influences the position of the peak and thus the optimal level of IE inflation, it is useful to examine also the limiting case $\epsilon = 0$, corresponding to a fixed longitudinal dimension $2b$. This is shown as a broken curve in the figure. The output now increases steadily with IE inflation, but is still reduced to near zero for a deflated IE. Finally, the dotted curve in the figure shows the result if we assume a value $\epsilon = 0.3$, which is probably rather larger than is appropriate in reality.

A. Comparison with open-beak calls

It is interesting to examine the acoustic reasons underlying the strategy of esophageal inflation in doves, as contrasted with simple vocalization through an open beak. Certainly the pure-tone nature of the dove coo provides clear species identification, but much of the reason for vocalization lies with the communication range achievable. How does the acoustic output from an inflated esophagus compare with that which the bird could achieve in an open-beak call?

The simplest way to examine this is to compare the acoustic power in each type of call with that which could be produced from the trachea and glottis tuned to the same frequency and simply vented to the environment. In all cases, glottis, beak or esophageal sac, the maximum dimensions of the radiating structure are small compared with the acoustic wavelength at the coo frequency of 600 Hz. A analysis treating the radiation as that from a “simple source” (Morse 1948; Fletcher 1992, ch. 7) therefore suffices, and the expression in (17) is an appropriate relative output measure.

A problem arises, however, in deciding what to keep constant in such a comparison. The actual acoustic power produced in any biological, or indeed musical, system is usually only a small fraction of the input power, which is in this case the product of the lung pressure (about 1.5 kPa) and the mean volume flow (about $10 \text{ cm}^3\text{s}^{-1}$), giving about 15 mW. The radiated acoustic power, on the other hand, is typically less than 1 mW or about 80 dB at a distance of 1 m. It is therefore reasonable to assume that, in terms of vocal effort, it is the total input power that should be kept constant in any comparison, rather than the acoustic input power, and this amounts to keeping the volume flow amplitude U_1 through the syrinx constant.

The analysis developed earlier in Section III can now be used to compare the acoustic outputs from the IE and from a simple vented glottis. The first case has already been calculated and displayed in the figures. To simulate radiation from the glottis in the absence of the IE, it is adequate to simply set the effective sac mass m equal to zero in the calculation. The result, when output power is plotted against frequency, is a peak similar to that in Fig. 4, but reduced in amplitude by a factor of about 12, corresponding to a decrease in radiated sound level of about 11 dB, and with a smaller peak at around 2300 Hz representing the mis-tuned second resonance of the trachea and glottal constriction.

A similar calculation is now, in principle, required for radiation from the beak. The beak is acoustically complex, however, even at low frequencies where beak resonances are not involved. The acoustic behavior of a beak model has, however, been investigated in detail by Fletcher and Tarnopolsky (1999), and their results show that, to a reasonable approximation, a partly opened beak imparts an acoustic power gain of about 6 dB, or a factor 4, compared with the power that would be radiated from the open glottis, assuming that the acoustic input power is the same in each case. If the total input power, rather than the acoustic power, is kept constant, then the beak gain will be rather less than this, say 4 or 5 dB.

From this analysis it is thus reasonable to conclude that the inflated-esophagus strategy gains the dove a significant advantage of about 6 dB in terms of radiated power at the fundamental coo frequency, compared with a normal call through the beak. This numerical value will depend upon the value of the quality factor Q of the IE resonance, increasing with increasing Q . The beak-radiated call will, however, also contain some power at higher harmonic frequencies that is filtered out by the IE. The IE coo possesses the probable advantage of being very different in acoustic spectrum from a typical beak-radiated call, which may aid in conspecific communication.

IV. CONCLUSIONS

This detailed analysis of the acoustics of the vocal system of the dove leads to several related conclusions, as follows.

- (i) The vocal tract as a whole is tuned to the fundamental frequency of the dove coo. This involves both passive anatomical tuning of the inflated esophageal sac and also active tuning by the bird of the glottal constriction coupling the trachea to the esophagus.
- (ii) To produce maximum acoustic output, the resonance frequency of the IE must be approximately matched to the song frequency. This matching depends upon the total vibrating mass of the IE walls and the degree to which the IE is inflated. The resonance frequency is, however, not critically dependent upon IE volume, so that the inflation caused during a single coo does not greatly affect this matching.
- (iii) To produce maximum acoustic power, the glottis must also be constricted so that

the resonance of the trachea with glottal termination approximately matches the song frequency.

- (iv) It is reasonable to suppose that young birds have to learn to constrict the glottis appropriately before they can produce satisfactory coos.
- (v) As well as eliminating upper harmonics to produce a characteristic pure-tone coo, the evolved strategy of radiating the coo of the dove by means of an inflated esophagus rather than an open beak gives a significant increase in radiated acoustic power, and thus in the range of audibility of the call.

The analysis reported here neglects the feedback influence of the vocal tract upon the syringeal oscillation. This coupling, the mechanics of which have been discussed elsewhere (Fletcher 1988), can be expected to magnify the resonance effects discussed here and to lead to an even closer dependence of power output upon glottal tuning.

While this analysis does not claim to resolve all the questions associated with dove calls, it does appear to provide a reasonable basis for understanding the origin of the almost pure-tone sound and the function of the glottal constriction. In passing, it could be noted that there is a surprising resemblance between the dove, with its inflated esophagus and pure-tone coo, and the bladder cicada *Cystosoma Saundersii* (Westwood), whose abdomen consists simply of a hollow ellipsoid, the resonance of which reinforces the fundamental of the 800 Hz sound generated by repeatedly buckling tymbals (Fletcher and Hill 1978).

Acknowledgment

T. Riede was supported by a fellowship within the Postdoctoral Programme of the German Academic Exchange Service (DAAD).

REFERENCES

- Ballintijn, M.R., ten Cate, C., Nuijens, F.W., and Berkhoudt, H. (1995). “The syrinx of the collared dove (it *Streptopelia decaocto*): structure, inter-individual variation and development,” *Netherlands J. Zool.* **45**, 455–479.
- Beckers, G.J.L., Suthers, R.A., and ten Cate, C. (2003a). “Pure-tone birdsong by resonance filtering of harmonic overtones,” *Proc. Nat. Acad. Sci.* **100**, 7372–7376.
- Beckers, G.J.L., Suthers, R.A., and ten Cate, C. (2003b). “Mechanisms of frequency and amplitude modulation in ring dove song,” *J. Exp. Biol.* **206**, 1833–1843.
- Casey, R.M. and Gaunt, A.S. (1985). “Theoretical models of the avian syrinx,” *J. Theor. Biol.* **116**, 45–64.
- Fletcher, N.H. (1988). “Bird song—a quantitative acoustic model,” *J. Theor. Biol.* **135**, 455–481.
- Fletcher, N.H. (1992). *Acoustic Systems in Biology*, (Oxford University Press, New York), Ch. 8–12.
- Fletcher, N.H. (2000). “A class of chaotic bird calls?” *J. Acoust. Soc. Am.* **108**, 821–826.
- Fletcher, N.H. and Hill, K.G. (1978). “Acoustics of sound production and of hearing in the bladder cicada *Cystosoma Saundersii* (Westwood)” *J. Exp. Biol.* **72**, 43–55.
- Fletcher, N.H. and Tarnopolsky, A. (1999). “Acoustics of the avian vocal tract,” *J. Acoust. Soc. Am.* **105**, 35–49.
- Greenwalt, C.H. (1968). *Bird Song: Acoustics and Physiology* (Smithsonian Institution, Washington DC).
- Kinsler, L.E., Frey, A.R., Coppens, A.B. and Sanders, J.V. (1982). *Fundamentals of Acoustics*, (Wiley, New York).
- Morse, P.M. (1948) *Vibration and Sound* (McGraw–Hill, New York; reprinted Acoustical Society of America, 1981) pp. 312–314.

Riede, T., Beckers, G., Blevins, W., and Suthers, R. (2004). "Esophagus inflation and vocal tract filtering in Ring doves," (submitted to *J. Exper. Biol.*)

Table I

length of trachea	$L = 75$ mm
diameter of trachea	$d = 3$ mm
length of glottal constriction	$l = 5$ mm
diameter of glottal constriction	$g = 0.8$ mm
diameter of inflated esophagus	$2a = 35$ mm
length of inflated esophagus	$2b = 50$ mm
fraction of IE surface vibrating	0.5
total mass of IE walls	$m = 2$ g
quality factor of IE resonance	$Q = 10$

FIGURE CAPTIONS

Figure 1. Simplified geometry of the vocal tract of the Ring dove.

Figure 2. (a) Electric network simulating the acoustic behavior of the vocal tract of the dove. Voltage is the analog of acoustic pressure, and current is the analog of acoustic volume flow. (b) More detailed representation of the analog impedances of the glottal constriction and the esophageal sac.

Figure 3. Calculated relative acoustic power output at 600 Hz as a function of the diameter of the glottal constriction, assuming the parameter values shown in Table I. The broken curve shows the result of reducing the effective mass of the IE walls to 1 g, thus increasing the IE resonance frequency.

Figure 4. Calculated relative power output as a function of coo frequency assuming the glottal constriction to be adjusted to the value given in Table I so as to optimize power output at 600 Hz. (The double peak is due partly to slight misalignment of resonance frequencies and partly to the series-parallel resonance arrangement shown in Fig. 2.) The broken curve shows the effect on power output of reducing the effective mass of the IE walls to 1 g, thus increasing the IE resonance frequency to about 900 Hz.

Figure 5. Calculated relative acoustic power at 600 Hz as a function of the IE lateral diameter $2a$, assuming that the expansion parameter $\epsilon = 0.1$ and that other parameters are as in Table I. The broken curve shows the calculated result if $\epsilon = 0$, so that the longitudinal dimension $2b$ of the IE remains constant during the expansion, while the dotted curve shows the result if $\epsilon = 0.3$.

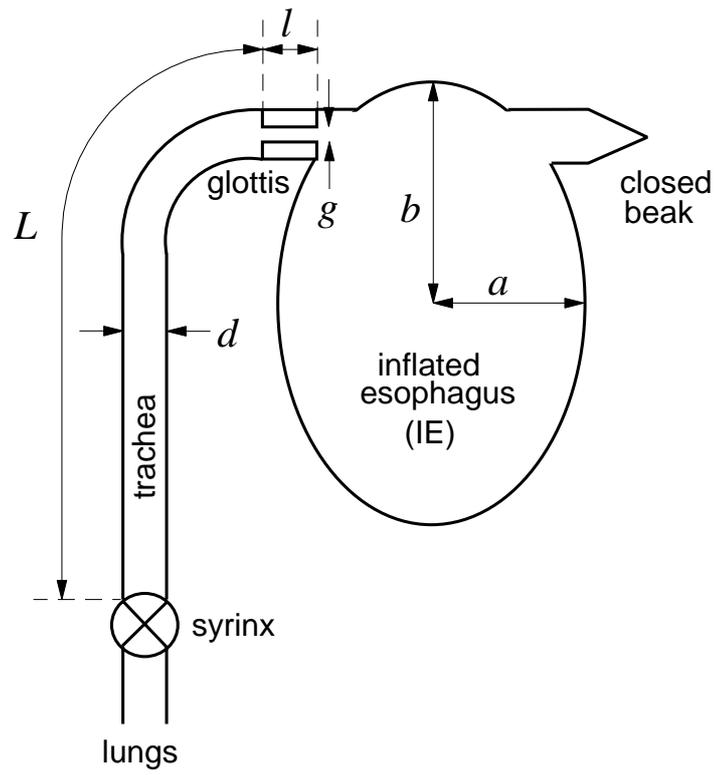


FIG. 1: Simplified geometry of the vocal tract of the dove.

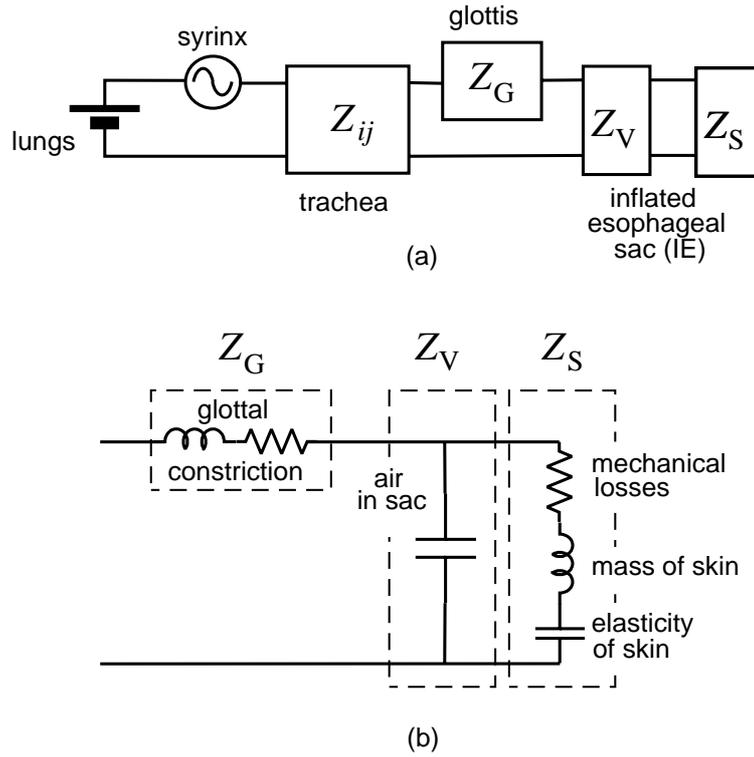


FIG. 2: (a) Electric network simulating the acoustic behavior of the vocal tract of the dove. Voltage is the analog of acoustic pressure, and current is the analog of acoustic volume flow. (b) More detailed representation of the analog impedances of the glottal constriction and the esophageal sac.

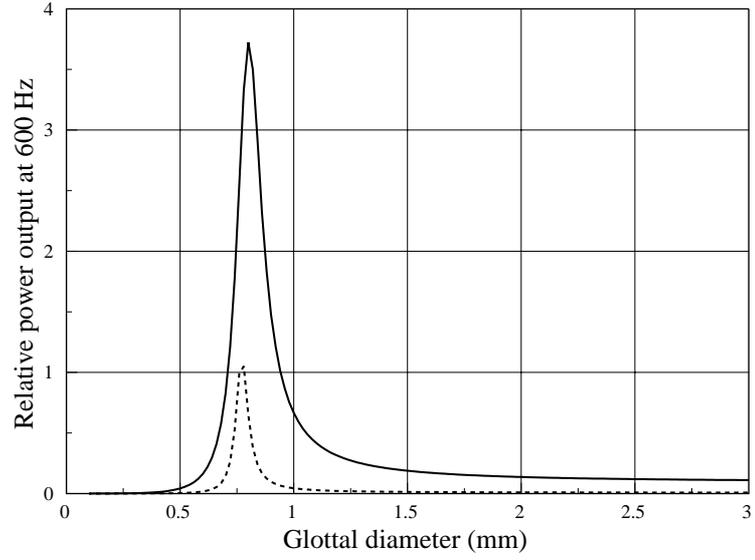


FIG. 3: Calculated relative acoustic power output at 600 Hz as a function of the diameter of the glottal constriction, assuming the parameter values shown in Table I. The broken curve shows the result of reducing the effective mass of the IE walls to 1 g, thus increasing the IE resonance frequency.

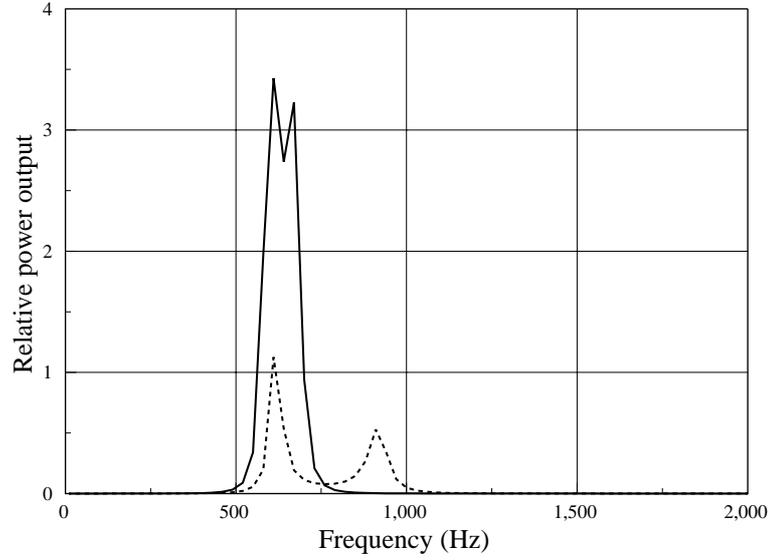


FIG. 4: Calculated relative power output as a function of coo frequency assuming the glottal constriction to be adjusted to the value given in Table I so as to optimize power output at 600 Hz. (The double peak is due partly to slight misalignment of resonance frequencies and partly to the series-parallel resonance arrangement shown in Fig. 2.) The broken curve shows the effect on power output of reducing the effective mass of the IE walls to 1 g, thus increasing the IE resonance frequency to about 900 Hz.

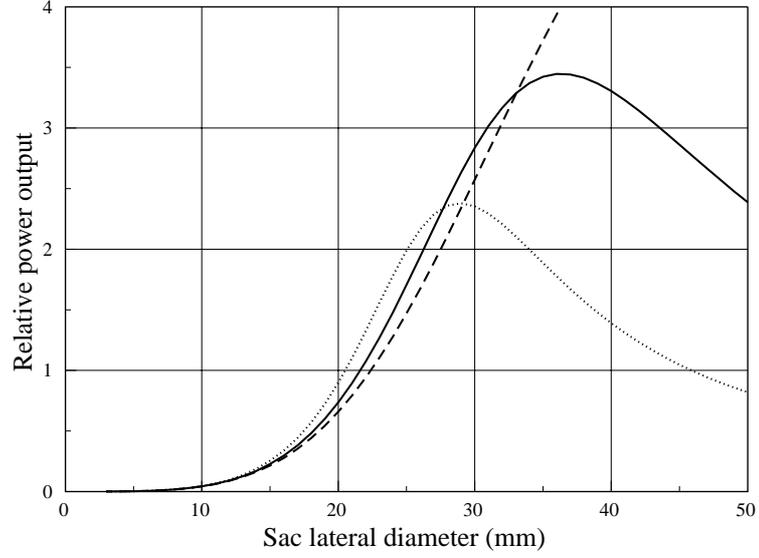


FIG. 5: Calculated relative acoustic power at 600 Hz as a function of the IE lateral diameter $2a$, assuming that the expansion parameter $\epsilon = 0.1$ and that other parameters are as in Table I. The broken curve shows the calculated result if $\epsilon = 0$, so that the longitudinal dimension $2b$ of the IE remains constant during the expansion, while the dotted curve shows the result if $\epsilon = 0.3$.