A Monthly e Magazine
ISSN:2583-2212
Popular Article
February, 2026 Vol.6(2), 495-501

Anatomy of the Avian Voice

Jhuma Debbarma[1], J B Rajesh[2], Bensia Debbarma[1], Jashima Debbarma[3], Zosangpuii[4]
[1]PG Scholar, Department of Veterinary Anatomy and Histology, College of Veterinary Sciences and Animal Husbandry, Central Agricultural University (Imphal), Selesih, Aizawl, Mizoram: 796015
[2]Associate Professor, Department of Veterinary Medicine, College of Veterinary Sciences and Animal Husbandry, Central Agricultural University (Imphal), Selesih, Aizawl, Mizoram: 796015
[3]PhD Scholar, Department of Veterinary Medicine, College of Veterinary Sciences and Animal Husbandry, Central Agricultural University (Imphal), Selesih, Aizawl, Mizoram: 796015
[4]Subject Matter Specialist, Livestock Production, Krishi Vigyan Kendra, Central Agricultural University (Imphal), Selesih, Aizawl, Mizoram: 796015
*Corresponding author: leovet@gmail.com
DOI:10.5281/ScienceWorld.18879781

Abstract

Birds produce sounds using a specialized anatomical structure called the syrinx. Variation in vocal ability among bird species reflects differences in syrinx morphology, musculature, neural control, and evolutionary adaptations. Vocalizing birds like songbirds (oscines) possess complex syringeal structures and neuromuscular control, while non-vocalizing or less vocal birds often have simplified syrinx anatomy or alternative sound mechanisms. Understanding these anatomical variations sheds light on avian communication evolution and ecological adaptations.

Keywords: Anatomy, Birds, Singing, Syrinx, Vocalizing

Introduction

Birds communicate a wide range of information through their vocal expressions. Birds use so-called cries to send various alerts about an approaching danger, identify individuals in a flock, demarcate and maintain territories, and so on. The call character implies that they are shorter and more effective voice expressions. Avian songs are another kind of avian vocal expressiveness. Most species are unable to be heard throughout the year (Beecher *et al*., 2005). They are often produced by male birds to signal a territory takeover and to summon females at the start of a nesting time. In general, a song is a more complicated vocal expression with a longer length than a call (Stastny *et al*., 2018).

Category	Bird	Maximum frequency
Highest overall	Oilbird	15-20 KHz (Catchpole and Slater, 2003)
Highest songbird (tonal)	Finecrest /Goldcrest	12-14 KHz (Catchpole and Slater, 2003)

Species	Type of Sound	Minimum/dominant frequency	Key anatomical adaptation
Southern Cassowary (*Casuarius casuaris*)	Deep boom / infrasonic call	20–32 Hz	Large body, elongated vocal tract, resonant soft tissues (Mack *et al*., 2003)
Emu (*Dromaius novaehollandiae*)	Drumming / booming	50–100 Hz	Inflatable neck (tracheal) sac acting as resonator (Baker *et al*, 2009)
Ostrich (*Struthio camelus*)	Roar / boom	<100 Hz	Long trachea, large thoracic air volume (Beckers *et al*., 2013)
Common Bittern (*Botaurus stellaris*)	Marsh boom call	100–200 Hz	Esophageal & tracheal inflation for resonance (Catchpole and Slater, 2003)

Avian Vocal Organ: The Syrinx

1. Syrinx Location and Basic Form

In both singing and non-singing birds, the syrinx lies at the tracheobronchial junction, within the interclavicular air sac. However, the type of syrinx differs:

In most oscine passerines (true songbirds), such as the Passeriformes, the syrinx is typically tracheobronchial in type. In this configuration, sound-producing tissues (medial and lateral labia or tympaniform membranes) are positioned at the bronchial bifurcation and are supported by modified tracheal and bronchial cartilages.

This arrangement enables the presence of bilateral sound generators, allowing independent control of the left and right bronchial sound sources. Such structural specialization forms the anatomical basis for complex acoustic phenomena, including rapid frequency modulation and simultaneous dual-tone production (Goller, 2022).

In contrast, many non-songbirds, including species within Columbidae (pigeons and doves) and Strigiformes (owls) possess a tracheal or relatively simpler bronchial syrinx. In these forms, the sound-producing membranes are fewer and often confined primarily to either the tracheal portion or a limited bronchial region. The supporting cartilaginous framework is less specialized, and bilateral independence is typically reduced or absent. Consequently, these species generally produce simpler, less modulated vocalizations compared to oscine songbirds (Legendre *et al*., 2024).

2. Sound Generators

In highly vocal species such as oscine songbirds (*e.g*., Passeriformes songbirds) within the order Passeriformes, the syrinx exhibits marked structural specialization. One of its most distinctive features is the presence of two independent sound generators, one located in each primary bronchus. These bilateral sound sources can function independently, allowing birds to produce two different frequencies simultaneously or to create rapid acoustic modulations. This dual-source mechanism provides the anatomical basis for the extraordinary acoustic complexity characteristic of many songbirds.

The syringeal lumen contains multiple vibrating tissues, including the medial and lateral labia and the medial tympaniform membranes (membrana tympaniformis medialis). These structures function analogously to mammalian vocal folds but demonstrate greater biomechanical flexibility. Sound production results from aerodynamic forces generated by expiratory airflow, which induce self-sustained oscillation of the membrana tympaniformis and associated syringeal tissues (Goller, 2022).

The pessulus, a median cartilaginous or ossified structure located at the bronchial bifurcation, provides structural support and contributes to airflow division between the two bronchial sound sources. This configuration establishes a self-oscillating aeroelastic system in which airflow, tissue elasticity, and muscular control interact to generate and modulate sound (Suthers and Zollinger, 2004).

Intrinsic syringeal muscles finely regulate vocal output by adjusting membrane tension, bronchial aperture, and labial positioning. Such precise muscular modulation enables complex frequency sweeps, amplitude variation, harmonic control, and nonlinear acoustic phenomena. In advanced vocal learners including parrots (order Psittaciformes), corvids such as crows (family Corvidae), and mynas (family Sturnidae), this anatomical sophistication supports the remarkable ability to mimic environmental sounds and even aspects of human speech (Elemans *et al*., 2015).

In contrast, many non-songbirds exhibit a comparatively simplified syringeal organization. These species often possess fewer or less differentiated vibrating membranes, sometimes relying on a single principal vibrating mass. Additionally, there is typically reduced bilateral differentiation between the left and right bronchial components of the syrinx, limiting independent sound production (Schonhofer and Gahr, 2025).

The intrinsic musculature is usually less complex, resulting in more restricted control over pitch modulation, amplitude variation, and harmonic structure. Consequently, vocal output in

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Published 28/02/2026

these birds generally consists of simpler calls rather than elaborate, learned songs (Schonhofer and Gahr, 2025).

3. Intrinsic and Extrinsic Musculature

Singing Birds

Vocal learners such as oscine songbirds possess an intricate muscle array:

6–8 pairs of intrinsic muscles that attach solely within the syringeal structure, enabling precise control of pitch, frequency modulation, and dynamics. The intrinsic syringeal muscles are collectively referred to as the tracheosyringeal muscles.

Musculus tracheosyringeus dorsalis (TD): Located dorsally; involved in controlling tension of the medial labia and fine pitch modulation.

Musculus tracheosyringeus ventralis (TV): Positioned ventrally; contributes to adduction and tension adjustment of the vibrating elements.

Musculus tracheosyringeus lateralis (TL): Found laterally; assists in regulating aperture and amplitude of sound production.

Musculus syringealis dorsalis (SD): Acts on the dorsal syringeal cartilages; important for subtle frequency control.

Musculus syringealis ventralis (SV): Modulates ventral labial positioning and airflow dynamics.

Musculus syringealis medialis (SM) (in some species): Provides additional fine control of medial labial tension.

In Song birds (brown thrashers, Toxostoma rufum, and cardinals, Cardinalis cardinalis), the dorsal muscles are the main adductors and the m. tracheobronchialis ventralis the main abductor. Their activity correlates with decreasing and increasing airflow through the syrinx, respectively. The largest syringeal muscle, m. syringealis ventralis, does not appear to gate airflow. However, it may regulate the tension of the syrinx.

The syringeal muscles are instrumental in preparing the syrinx for phonation by moving the labia or lateral tympaniform membranes into the airway and tensing the syrinx appropriately (Elemans, 2006).

Non-Singing Birds

Non-songbirds typically exhibit fewer intrinsic syringeal muscles and greater reliance on extrinsic muscles and simpler respiratory pressure for producing basic vocalizations (calls, coos). In the non-singing bird's syrinx have suggested that the intrinsic muscles, m. syringealis superficialis and m. syringealis profundus, are arranged as antagonists, whose action narrows and widens the syringeal lumen, respectively (Larsen and Franz, 2002).

4. Neural Control of the Syrinx and Vocal Motor Pathways in Singing and Non-Singing Birds

Neural Control in Singing Birds (Vocal learners)

Vocal learning birds especially oscine songbirds within Passeriformes possess a discrete and well-organized song control system in the forebrain.

4.1 Forebrain Song System

The vocal motor pathway includes:

I. HVC (High Vocal Centre): a premotor nucleus initiating patterned song sequences
II. RA (Robust nucleus of the Arcopallium): a motor nucleus projecting to brainstem vocal neurons
III. Anterior Forebrain Pathway (AFP): including nucleus Area X, dorsolateral thalamus (DLM), and lateral part of the magnocellular nucleus of the anterior neostriatum (LMAN), essential for vocal learning and plasticity

The motor production pathway proceeds:

HVC → RA → nucleus of the twelfth cranial nerve, tracheosyringeal part (nXIIts) → Syringeal muscles

The final common pathway for vocal output is the tracheosyringeal portion of the hypoglossal motor nucleus, located in the caudal medulla. Motor neurons send axons via the tracheosyringeal branch of the hypoglossal nerve to intrinsic syringeal muscles.

Song birds exhibit:

i. Highly differentiated motor neuron pools
ii. Fine motor unit organization
iii. Precise bilateral coordination of syringeal muscles
iv. Strong forebrain-to-brainstem descending projections

This organization allows rapid frequency modulation, independent bilateral control of sound generators, and learned acoustic patterning (Wild, 2004; Schmidt and Wild, 2014).

Neural Control in Non-Singing Birds (Innate Vocalizers)

Non-songbirds (*e.g.*, pigeons, chickens, many waterfowl) lack the elaborate forebrain song nuclei found in vocal learners.

4.2 Absence of Forebrain Song Circuitry

In these species:

HVC and RA homologous structures are absent or not functionally specialized for vocal learning. There is no anterior forebrain learning pathway comparable to the AFP

Vocal control is primarily mediated by:

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i. Brainstem respiratory-vocal networks
ii. The hypoglossal motor nucleus (including nXIIts)
iii. Nucleus ambiguus (laryngeal control)

Although the syrinx still receives motor innervation from nXIIts, the absence of strong telencephalic descending input limits voluntary modulation and learning capacity. Consequently, vocalizations are:

i. Innate rather than learned
ii. Less acoustically complex
iii. More dependent on respiratory rhythm generators

Studies of non-songbirds demonstrate simpler motor neuron organization and reduced bilateral independence compared to oscines (Elemans *et al*., 2007; Wild, 2004).

Conclusion

Singing birds exhibit a tracheobronchial syrinx with bilateral sound generators, multiple intrinsic muscles, and a specialized forebrain song system enabling vocal learning and acoustic complexity. In contrast, non-singing birds possess simpler syringeal structures, reduced intrinsic musculature, and lack dedicated telencephalic song nuclei. These anatomical and neural differences collectively explain the profound divergence in vocal flexibility and complexity across avian taxa.

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