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Anatomy of the upper respiratory tract in domestic birds, with emphasis on vocalization

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With 16 figures

Short title: Avian vocalization
Abstract

This work reviews the anatomy of the upper respiratory tract in domestic birds including the chicken and pigeon. Non-exhaustive additional information on other bird species, illustrating the extraordinary diversity in the biological class *Aves*, can be found in several footnotes. The described anatomical structures are functionally considered in view of avian sound production. In particular the *Syrinx* is invaluable. Its most important structures are the *Labia* and the lateral and medial tympanic membranes in non-songbirds and songbirds, respectively. These structures produce sound by vibrating during expiration and eventually inspiration.

Key words: Bird; Anatomy; Upper respiratory tract; Vocalization
ANATOMY OF THE UPPER RESPIRATORY TRACT

Nasal cavity

The nasal cavity (Cavitas nasalis) of the chicken (Gallus gallus domesticus) and pigeon (Columba livia domestica) is dorsally bordered by the frontal process (Processus frontalis) of the incisive bone (Os incisivum syn. Os premaxillare), the intermaxillary process (Processus intermaxillaris) of the nasal bone (Os nasale), and the lacrimal bone (Os lacrimale). The lateral border is delineated by the maxillary process (Processus maxillaris) of the nasal bone. The floor of the nasal cavity is formed rostrally by the maxillary process of the incisive bone and caudally by the palatine bone (Os palatinum).

The large orbits limit the nasal cavity caudally (Fig. 1).

In most avian species, the nasal openings (Nares) are located dorsolaterally at the basis of the upper beak. In the chicken, they are enclosed by a dorsal and ventral cartilaginous plate. Both plates join at their caudal borders where a shallow internal niche is formed (Fig. 2). The dorsal cartilaginous plate is covered by keratinized epithelium denoted as the Operculum (McLelland, 1990). Furthermore, it may be raised by the cere (Cera) in some species, such as the domestic pigeon and the budgerigar (Melopsittacus undulatus) (Fig. 3). In the latter species, the colour of the cere is gender-dependent.

The nasal openings are connected to the nasal cavity where the inhaled air is filtered from the larger particles, warmed and moisturized (Fedde, 1998). In fowl, the nasal cavity can be divided into the rostral Vestibulum nasi and the caudal Cavum nasi proprium. The former structure is lined by a squamous epithelium (Nickel et al., 1977) and is encircled by a curved lamella that projects mediorostrally from the caudal part of the dorsal cartilaginous plate, which partly covers the nasal opening, towards the nasal
The inhaled air flows medial to the lamella of the upper cartilaginous plate and lateral to the nasal septum to reach the nasal cavity. In most avian species, including the chicken and pigeon, the nasal cavity contains a ventral and dorsal nasal concha (Fig. 5). The ventral nasal concha (Concha nasalis ventralis) is larger, more rostrally situated and consists of a thin cartilaginous lamella lined by a mucociliary respiratory epithelium (Fig. 6). This concha arises from the dorsolateral wall of the nasal cavity and extends in caudoventral direction towards the choanae (Fig. 5). Ventral to the ventral nasal concha, the nasolacrimal duct (Ductus nasolacrimalis) discharges into the nasal cavity by a slit-like opening (Nickel et al., 1977). The smaller dorsal concha (Concha nasalis dorsalis) originates on the ethmoid bone and projects into the nasal cavity (Fig. 5). Its rostral part is covered by a mucociliary epithelium, whereas the caudal part is lined by an olfactory epithelium involved in odour perception (Fitzgerald, 1969). This concha is absent in the pigeon (Nickel et al., 1977).

The pyramidal infraorbital sinus (Sinus infraorbitalis) is lined by a very thin mucosa and lies lateral to the nasal cavity, rostroventral to the eye and caudal to the maxillary process of the nasal bone. The infraorbital sinus is connected to the cavity enclosed within the dorsal nasal concha by a mediodorsal fissure, which is broad in the

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1 In aquatic birds, such as the duck (Anas platyrhynchos), the nasal septum presents a large aperture (Nares perviae) (King and McLelland, 1975).
duck and goose (*Anser anser*) but narrow in fowl. Communication with the nasal cavity takes place through a more ventral cleft in the medial mucosal wall of the infraorbital sinus (Nickel et al., 1977) (Figs. 4 and 5). The rostral compartment of the sinus is covered by a squamous epithelium, whereas a ciliated cuboidal epithelium that comprises some goblet cells lines the more spacious caudal part of the sinus (McLelland, 1990).

The nasal cavity is connected with the oral cavity through the palatine or choanal cleft (*Choanae*) that presents as a slender fissure in the palate. Above this fissure lies the antorbital fossa (*Fossa antorbitalis*) that contains the infraorbital sinus (Fig. 6). The infundibular cleft (*Rima infundibuli* syn. *Tuba auditiva communis*) is located caudal to the choanal cleft (Fig. 3). Here, both auditory tubes (*Tubae auditivae*) originate by a common cavity (*Infundibulum tubarum*). The soft tissues surrounding the choanae and infundibular cleft contain lymphoid tissue that corresponds with the pharyngeal tonsil (Fig. 7) (Salomon and Krautwald-Junghanns, 2008; Casteleyn et al., 2010).

**Larynx**

The inhaled air that leaves the nasal cavity flows through the choanal cleft towards the larynx (*Larynx cranialis*), which hampers the entering of larger particles into the trachea. It consists of a short cylindrical structure that is composed of osseous, cartilaginous and musculomembranous components (Fig. 8). Maceration of the soft tissues reveals the presence of laryngeal osseous plates (Fig. 9). In addition, only the cricoid cartilage (*Cartilago cricoidea*) and paired arytenoid cartilages (*Cartilago arytenoidea*) are present in birds. No epiglottis nor a thyroid cartilage (*Cartilago thyroidea*) can be found (King and McLelland, 1975). The cricoid is composed of a semi-circular ventral cricoid plate
and dorsolateral wings that are connected to the plate by means of fibrous tissue. As such, it forms a ring of fibrocartilaginous/-osseous tissue. The arytenoid cartilages articulate dorsally with the cricoid. They are composed of a caudal, ossified rod-like part and a thin, cranial cartilaginous part that protrudes in cranial direction. The glottis (aditus laryngis) that forms the entrance to the larynx is located in between both arytenoids on the mons laryngis, which deviates the passage of fluids laterally, thus avoiding choking (Fig. 9). The dimensions of the larynx can be adjusted by laryngeal muscles (Nickel et al., 1977).

**Trachea**

The trachea originates at the larynx (Larynx cranialis) and is caudally connected to the Syrinx or Larynx caudalis. Along its entire length, the trachea is located in the median plane and is lined by a pseudostratified ciliary epithelium that contains some goblet cells. It crosses the crop dorsally and enters the thoracic cavity between the rami of the Furcula (Fitzgerald, 1969; Nickel et al., 1977). The oesophagus initially lies dorsal to the trachea, but deviates to the right towards the cranial thoracic aperture (Fig. 10).

The length of the trachea varies between different bird species. The trachea of the chicken consists of more than 100 closed tracheal rings or Anuli tracheales. Since these tend towards early ossification, the term Cartilagines tracheales seems less appropriate. The consecutive tracheal rings are connected to each other by elastic membranes (Ligamenta anularia). Moreover, the rings overlap well since they comprise a narrow and a wide part that are alternatingly located at the dorsal and ventral side (Fitzgerald, 1969).

Furthermore, the tracheal rings are interconnected by several muscles. The thin, striated Musculus (M.) tracheolateralis runs bilaterally along the entire length of the
trachea, thus from the *Larynx cranialis* to the *Larynx caudalis* (McLelland, 1990). In the chicken and pigeon, the left and right *M. sternotrachealis* originate on the craniolateral aspect of the sternum and insert ventrally on the trachea in the median plane, just cranial to the syrinx (McLelland, 1990) (Fig. 1).²

**Syrinx**

*Definition*

The *Syrinx*, also called the *Larynx caudalis*, is in most bird species invaluable in sound production. It is located at the bifurcation of the trachea into the primary bronchi. Its anatomic position is intrathoracic at the basis of the heart, which is at the level of the first and second thoracic vertebrae (Suthers et al., 1999, Larsen and Goller, 2002, Çevik-Demirkan et al., 2007) (Fig. 11). Furthermore, it is surrounded by the clavicular air sac (Vollmerhaus and Sinowatz, 1992).

According to its structural components, three syringeal types can be identified, viz. a tracheal, tracheobronchial and bronchial syrinx (King, 1979). The majority of bird species, including the chicken, the turkey (*Meleagris gallopavo*), the pigeon and mallard possess a tracheobronchial syrinx that is characterized by modifications of both the trachea and the primary bronchi (Yildiz et al., 2003; Suthers and Sollinger, 2004).³

**Osseous and cartilaginous structures**

² In several bird species belonging to the *Anserinae* (e.g. geese (genus *Anser* and *Branta*) and swans (genus *Cynus*)), *Gruidae* (crane birds), and *Paradisaeidae* (birds-of-paradise), the trachea is elongated, allowing for the formation of curves, curls and coils (Fig. 12). This conformation enables vocalizations that contain louder, lower frequency sounds (Clench, 1978; Frith, 1994; Daley and Goller, 2004).

³ The tracheal syrinx in the order *Passeriformes* (perching birds to which the suborder of the *Ocines*, i.e. the true songbirds, belong) or the bronchial syrinx that is present in the common cuckoo (*Cuculus canorus*) shows adaptations of only the trachea or bronchi, respectively (King, 1979).
The syrinx is supported by a number of cartilaginous rings (Cartilagines syringeales) that succeed the proper tracheal rings and are consequently termed tracheal syringeal rings (Cartilagines tracheales syringis) (Figs. 11, 13 and 14) (King and McLelland, 1975). These are closely assembled and as such form a firm cylindrical structure known as the Tympanum (King, 1979). Furthermore, they are closed annular structures, just like the proper tracheal rings. Their number varies considerably according to the species (eight in the chicken, up to 78 in some members of the Ciconiidae) (King, 1979). Ossification is possible in a few species such as the chicken, silver lark (Larus argentatus) and songbirds (Vollmerhaus and Sinowatz, 1992).

The more caudal syringeal cartilaginous rings are called bronchial syringeal rings (Cartilagines bronchiales syringis) and arise from the tympanum and form the basis of the partitioned tracheobronchial. As a consequence, they are paired (King and McLelland, 1975). These cartilaginous rings are not entirely closed, but have a C-like shaped profile (King, 1979, Çevik-Demirkan et al., 2007). The free margins face the median plane and support the Membrana tympaniformis medialis or interna (King, 1979). Where both medial tympaniform membranes join cranially, the Pessulus, i.e. a pyramidal wedge-shaped cartilage, can be observed in many bird species including the chicken and pigeon. This structure is, however, absent in the oscine songbirds (King and McLelland, 1975; King, 1979; Çevik-Demirkan et al., 2007) (Fig. 14).

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4 The Bulla syringealis or Bulla tympanica is a confined expansion of the syrinx that is present in some species (Fig. 15). The archetypal tympanic bulla of the drake is a bell-shaped extension at the left side of the syrinx that can present partial or complete ossification. It allows for the sound to resonate and as such amplifies the volume of the produced sound (King and McLelland, 1975; Vollmerhaus and Sinowatz, 1992).
Ligaments

A connective tissue strand links the medial aspects of the rostral parts of the left and right primary bronchi. This *Ligamentum interbronchiale* is called *Bronchidesmus* by King and McLelland (1975). The cavity enclosed by the tracheal bifurcation cranial to this ligament is the *Foramen interbronchiale* (King, 1979) (Fig. 14).

Membranes

The *Membrana tympaniformis lateralis* or *externa* is located bilaterally in the lateral walls of the syrinx at the level of the tracheobronchial junction (Fitzgerald, 1969). It can either extend from the *Tympanum* to the first bronchial rings, as in the chicken and the pigeon (Vollmerhaus and Sinowatz, 1992; Yildiz et al., 2003; Gaban-Lima and Höfling, 2006; Pierko, 2007) (Fig. 14), or can be composed of multiple short membranes that are located in between the successive bronchial syringeal rings (King, 1979). It lacks in the duck while its presence is controversial in perching birds (King, 1979).^5^ The *Membrana tympaniformis medialis* bilaterally bridges the *Pessulus* and the medial side of the primary bronchi. It dorsoventrally connects the medial free margins of the bronchial syringeal rings (Yildiz et al., 2003; Kabak et al., 2007). Both membranes form the lateral walls of the *Foramen interbronchiale* (Fig. 14).

The *Labia* are paired elastic strings located within the lateral and medial tympaniform membranes (King, 1979; Suthers and Zollinger, 2004; Çevik-Demirkan et

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^5^ In the tracheal syrinx type, the membrane is modified and accordingly termed *Membrana trachealis* (King, 1979).
These strings are in many cases the major source of sound (Frank et al., 2006).6, 7

Muscles

The description below makes use of the nomenclature presented in the Nomina Anatomica Avium (King, 1979). An alternative terminology that complicates the comprehension of the anatomy of the muscles involved in sound production can, however, be found in several literature reports. Nevertheless, two important clusters of muscles can be distinguished, i.e. the Mm. tracheales and the Mm. syringeales. The latter consist of intrinsic syringeal muscles, which have their origin and insertion on the syrinx. Extrinsic syringeal muscles have an attachment beyond the syrinx (King, 1979) and include some of the tracheal muscles.

The Mm. tracheales comprise the M. tracheolateralis, M. sternotrachealis, M. cleidotrachealis and M. sternohyoideus. The presence of this entire repertoire in a particular species is exceptional. In most non-songbirds, which possess a tracheobronchial syrinx type, only the M. tracheolateralis is described. Moreover,

6 Labia lack in some bird species, such as the silver lark and the long-legged buzzard (Buteo rufinus) (King, 1979; Kabak et al., 2007).

7 In addition to the here-described syringeal components, specific structures may be present in other avian species. In the common quail (Coturnix coturnix), the mucosal membrane that covers the Pessulus protrudes into the tracheal lumen. As a result, a Membrana semilunaris is formed (Fitzgerald, 1969; Frank et al., 2006). Since this structure cannot vibrate, it may play no role in sound production, in contrast to what was previously accepted (Frank et al., 2006). The Membrana tracheosyringealis is a paired membrane that is especially present in Columbiformes and Psittaciformes (King, 1979). This membrane covers the inner wall of the trachea caudally and attaches to the Tympanum and the first bronchial rings (Gaban-Lima and Höfling, 2006). The Valvula syringealis that is present in diving ducks (Aythyinae) and mallards (Anatinae) is a caudally oriented valve that originates on the inside of the lateral wall of the right primary bronchus. During diving, the contraction of the sternotracheal muscle allows for this valve and the medial tympaniform membranes to protrude into the bronchial lumina and almost entirely block the airflow through both primary bronchi (Frank et al., 2006).
Ratites, *Ciconiidae*, *Cathartidae* and some *Galliformes* lack tracheal muscles (King, 1979; Brackenbury, 1980; Gaunt, 1983; Yildiz et al., 2003; Frank et al., 2006; Çevik-Demirkan et al., 2007). The chicken and the pigeon possess both the *M. sternotrachealis* and *M. tracheolateralis* that both are extrinsic syrinx muscles (King, 1979; Brackenbury, 1980; Vollmerhaus and Sinowitz, 1992) (Fig. 16). Most domestic bird species such as the chicken and pigeon lack intrinsic syrinx muscles. However, some smooth muscle cells are present in the inter-bronchial area in the duck (Frank et al., 2006).

VOCALIZATION

Introduction

Mammals most commonly produce sound by means of their vocal cords that are bilaterally present in the larynx. Although the latter structure is also found in birds, vocal cords are lacking in these animals. Most bird species rely on their syrinx to vocalise.9

According to the species, the vocal repertoire of birds varies from simple sounds to more complex songs (Marler and Hamilton, 1966). Several functions can be attributed to the birdsong, such as territory marking and socialisation of the offspring in female

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8 *Passeriformes*, *Psittaciformes* and the oilbird (*Steatornis caripensis*) possess well-developed *Mm. syringeales* in addition to the tracheal muscles. Syrinx muscles are short and poorly delineated. They include the *Mm. tracheobronchialis dorsalis, ventralis et brevis* and the *Mm. syringealis dorsalis et ventralis* (King and McLelland, 1975; King, 1979; Sherwood et al., 2004; Gaban-Lima and Höfling, 2006).

9 Since the syrinx is absent in some members of the *Ratites* it is not surprising that they are deficient in voice production. However, some species generate sound using the beak. Several species of woodpeckers (*Picidae*) drum on tree-trunks to mark their territory. Storks (*Ciconiidae*), on the other hand, clatter by rapidly opening and closing the beak. Besides the beak, feathers can generate sound as well. This is the case in a.o. the white-bearded manakin (*Manacus manacus*), the common snipe (*Gallinago gallinago*) and hummingbirds (*Trochilidae*). The sound can either originate from wing snapping or from air turbulence around the feathers (Vuilleumier, 2002, Clark et al., 2011).
birds, and the luring of a mating partner in male birds. Additionally, it plays a role in the reproductive cycle and the recognition of family members (Marler and Hamilton, 1966; Gorissen and Eens, 2005). The text below focuses on sound production in the syrinx.

**The mechanism of sound generation**

In non-songbirds, such as the chicken and the pigeon, the lateral tympaniform membranes are responsible for the produced sound (Elemans et al., 2008). The classical model states that these membranes are initially relaxed, but when the air flows through the syrinx during expiration, the membranes present a cyclic vibration that is the result of the Bernoulli forces created by the airflow and the elastic restoring forces of the membrane itself (Gaunt, 1983; Ballintijn and Ten Cate, 1998). In this model, the pitch of the generated sound depends on the tension of the membranes, whereas the volume is related to the amplitude of the vibration (Gaunt, 1983). The structures that can influence these parameters are described below.\(^\text{10}\)

\(^{10}\) Extrapolating the classical model to songbirds holds that the medial tympaniform membranes are the sound generating structures since songbirds do not possess lateral tympaniform membranes. However, the fact that songbirds are still able to produce sound after their medial tympaniform membranes have been cut surgically could mitigate against the validity of the classical model in these bird species (Goller and Larsen, 1997b). After surgery, the sound is of lower intensity but the individual sounds are still mutable (Goller and Larsen, 1997b; 2002). Because of this observation, endoscopic research has promoted the labial hypothesis or the pulse-tone model that is most probably valid for a large number of songbird species (Goller and Larsen, 1997a; Suthers and Zollinger, 2004). Prior to the production of the sound, the syrinx is displaced in cranial direction and stretched. Consequently, the bronchi and the medial tympaniform membranes are stretched (Goller and Larsen, 2002). The Bernoulli forces that arise during expiration result in the subsequent displacement of the lateral and medial labia towards the lumina of the bronchi (Goller and Larsen, 1997a; 2002; Larsen and Goller, 2002). Due to their elasticity, a self-oscillating system, referred to as a pneumatic valve, is set in place (Goller and Larsen, 2002).

An alternative hypothesis is the whistle hypothesis that is based on aerodynamic principles. This model aims to clarify the production of tonal sounds in the collared dove (*Streptopelia decaocto*) (Ballintijn and Ten Cate, 1998; Goller and Larsen, 2002). When air travels at high velocity through a narrow passage, i.e. the syringeal opening (Fig. 14), turbulences arise in the airflow that, as in a whistle, act as sound generators (Gaunt, 1983; Ballintijn and Ten Cate, 1998). However, recent studies have rejected this model because the fundamental frequency of the produced tones failed to shift upwards when birds inhaled a lighter gas. Moreover, it was observed in the ring dove (*Streptopelia risoria*) that the tracheal and syringeal muscles have a major impact on the sound production (Elemans et al., 2004; 2006).
Influence of the musculature

Non-songbirds usually have no or only minor intrinsic syringeal muscles (King, 1979; Frank et al., 2006). The sternotracheal and tracheolateral muscles, both extrinsic syringeal muscles, have antagonistic mechanical effects. The tracheolateral muscle indirectly abducts or tenses the lateral tympaniform membrane by retracting the syrinx in cranial direction. The sternotracheal muscle, on the other hand, directly adducts or relaxes the membrane by drawing the trachea caudally (Gaunt and Gaunt, 1977; Suthers and Zollinger, 2004; Elemans et al., 2006). During the trill of the ring dove, the lateral tympaniform membranes are adducted and abducted in and out the syringeal lumen at a frequency of 24 Hz (Elemans et al., 2004; 2006).\(^{11}\)

Influence of the respiration

In the majority of avian vocalizations, the sound is produced during expiration (Suthers et al., 1999; Suthers and Zollinger, 2004). This can especially be appreciated when observing the crowing of the rooster, which is limited in time. The ring dove and the zebra finch, however, can also generate inspirational sounds (Gaunt et al., 1982; Goller

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\(^{11}\) In songbirds, the *M. tracheolateralis*, which ends in front of the syrinx (McLelland, 1990), stretches the syrinx and fits it in the appropriate position for sound production (Goller and Larsen, 1997a; Larsen and Goller, 2002). The *M. syringealis dorsalis* and the *M. tracheobronchialis dorsalis* adduct the medial and lateral labia, which results in the narrowing of the syringeal aperture (Elemans et al., 2006). This is important for the timing of the vocalisation within the appropriate phase of the respiratory cycle (Larsen and Goller, 2002; Suthers and Zollinger, 2004). The *M. tracheobronchialis ventralis* has the opposite function (Larsen and Goller, 2002). The lateral part of the *M. syringealis ventralis* mainly influences the tension on the labia. As a result, this muscle has impact on the pitch of the produced sound (Suthers and Zollinger, 2004). Finally, the *M. sternotrachealis* holds the syrinx in a stable position during the strong contractions of the intrinsic syringeal muscles that are necessary for the generation of high tones (Goller and Suthers, 1996).
During expirational sound production, the expiratory muscles generate a specific airflow and pressure that are bilaterally present in the syrinx, even though the sound might be produced unilaterally, a phenomenon known as lateralisation of the sound production (Suthers and Zollinger, 2004).12

**Influence of the suprasyringeal structures**

The sound waves that are generated in the syrinx are modified through their way out by the trachea, the oropharyngeal-oesophageal cavity, the tongue and the beak (Suthers et al., 1999; Beckers et al., 2004; Riede et al., 2006). The trachea mutes or amplifies some frequencies. As mentioned above, the tracheas of geese and swans, crane birds and birds-of-paradise present curves, loops or windings (Fig. 12) that allow for generating louder sound of lower frequency (Clench, 1978; Frith, 1994; Daley and Goller, 2004). The larynx and the hyoid bone can modify the volume of the initial segment of the oesophagus (Riede et al., 2006). When low frequency sounds are produced, the oesophagus and the oropharynx present a single cavity, i.e. the oropharyngeal-oesophageal cavity. Its volume decreases when higher frequency sounds

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12 Songbirds possess two independent sound sources because the musculature of each syringeal side is innervated by the ipsilateral Nucleus n. hypoglossi (Suthers et al., 1999; Wild et al., 2000). Both sources can function simultaneously or independently (Suthers et al., 1999). Some bird species switch between both sides or use both sides simultaneously (Suthers, 2001). Since the tones that are produced in the right side of the syrinx, which has a smaller diameter bronchus (Luine et al., 1980), have a higher frequency, the bird can cover a wider range of frequencies (Suthers, 2001). This two-voice system is also present in non-songbirds such as the king penguin (Aptenodytes patagonicus) and the emperor penguin (Aptenodytes forsteri) that are able to produce specific calls that can be recognized individually (Aubin et al., 2000).

Other species have a preference for one side of the syrinx (Wild et al., 2000; Suthers, 2001; Wade et al., 2002). If, for example, the left side of the syrinx produces sound during expiration, the right side is closed, but it opens after each syllable for a short inspiration. The longer the syllable, the longer the duration of the inspiration is (Suthers and Zollinger, 2004). When a high number of sound elements has to be generated, which is typical in the canary (Serenus), a pulsating respiration is performed. Sound is produced by repeatedly opening and closing one side of the syrinx, allowing the passage of air pulses that are each associated with one syllable (Suthers et al., 1999). The advantage of the mini-respiration lies in the fact that the bird can continue singing for longer periods.
are generated (Suthers, 2006). The degree of opening of the beak during vocalization is positively correlated with the frequency (Suthers et al., 1999). The tongue might seem of minor importance since it is a rather rigid structure that is not suitable for articulation, as in humans (Wild, 2004). However, it was recently demonstrated in northern cardinals (Cardinalis cardinalis) that tongue elevation lowers the resonance frequency below 2 kHz by reducing the area of the passage from the oral cavity into the beak (Suthers et al., 2016). The tongue of Psittaciformes is exceptional as it can change the amplitude and frequency of the sound. This partly explains their capacity of mimicking the human speech (Beckers et al., 2004).

CONCLUSIONS

Vocalization in birds is the result of the flawless synchronisation of the respiration and the muscle activation in the upper respiratory tract. In most species, the sound is created during expiration by the vibrations of the membranes and Labia that are present in the syrinx. Although the main principles of sound production in birds are well known, it should be noticed that variations exist in the fine-tuning of the singing between species. Moreover, the anatomy of the sound producing organs is variable as well.

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Conflict of interest statement
None declared.

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Figures

Fig. 1. Left lateral view of the skull of a chicken showing the bony limitations of the nasal cavity. 1 = incisive syn. premaxillary bone, 1’ = frontal process, 1” = maxillary process, 2 = maxillary bone, 3 = nasal bone, 3’ = intermaxillary process, 3” = maxillary process, 4 = lacrimal bone, 5 = palatine bone

Fig. 2. Left ventrolateral views of the left nasal opening of a chicken. A: The dorsal (1) and ventral (2) cartilaginous plate surround the nasal opening. Where they join caudally, a niche (asterisk) is formed. A lamella (3) branches off from the dorsal cartilaginous plate, which is also called the operculum. B: After detaching the operculum rostrally, the lamella becomes obvious.

Fig. 3. Rostral view of the head of a pigeon showing the cere (1) at the basis of the upper beak which borders the nasal openings caudally (2). The widely-opened beak allows for inspection of the choanal cleft (3) and the infundibular cleft (4). Adapted from Casteleyn et al. (2011b)

Fig. 4. Left lateral view of the head of a chicken. The cartilages surrounding the nasal opening have been removed showing the cartilaginous nasal septum (1). The infraorbital sinus (2) is visible in between the maxillary process of the nasal bone and the eye. The probe shows the cleft through which the infraorbital sinus communicates with the nasal cavity.
Fig. 5. Left lateral view of the head of a chicken visualising the nasal cavity. A: The cartilages of the nasal opening and the maxillary process of the nasal bone have been removed, showing the nasal septum (1) and the antorbital fossa (2) that lies dorsal to the palatine cleft. The infraorbital sinus (3) has been opened. B: After removal of the nasal septum, the medial aspect of the right nasal cavity becomes visible. The lamella of the right operculum (4), the large ventral nasal concha (5) and the small dorsal nasal concha (6) can be observed. The level at which the histological cross-section of the nasal cavity shown in Fig. 6 is made is indicated by the double arrow.

Fig. 6. Histological cross section of the nasal cavity of the chicken (decalcified specimen; original size: 125 mm x 90 mm) at the level of the corners of the beak. 1 = nasal septum, 2 = antorbital fossa, 3 = dorsal nasal meatus, 4 = cavity of the dorsal nasal concha, 5 = infraorbital sinus, 6 = nasolacrimal duct, 7 = frontal bone, 8 = palatine bone, 9 = jugal bone

Fig. 7. Longitudinal histological section (haematoxylin-eosin staining) of the palate of a chicken showing the presence of lymphoid tissue in the nasal mucosa bordering the choanal and infundibular clefts. Some lymphoid follicles are indicated by the arrows. Adapted from Casteleyn et al. (2010)

Fig. 8. Dorsal view of the larynx (1) and cranial segment of the trachea (2) of the chicken. The slit-like laryngeal entrance that is flanked by the protruding arytenoid cartilages (asterisks) is indicated by the arrow.
Fig. 9. Craniolateral view of a macerated larynx of a chicken showing the laryngeal cartilages that are highly ossified in this specimen. The entrance to the larynx is indicated by the arrow. The cricoid is composed of the ventral cricoid plate (1) and the dorsolateral wings (2). The fibrous tissue that connects both parts has been macerated. Its localisation is indicated by the asterisk. The paired arytenoid cartilage consists of a rod-like caudal part (3) and a thin cartilaginous cranial part (4).

Fig. 10. Ventral view of the neck of a chicken showing the localisation of the trachea (1), oesophagus (2) and crop (3).

Fig. 11. Ventral views of the thoracic cavity of a pigeon after removal of the sternum. A: The syrinx presents an intrathoracic localisation at the level of the first two thoracic vertebrae. It is covered ventrally by the basis of the heart. B: After caudal retraction of the heart, the syrinx (boxed) that is located at the tracheal bifurcation becomes visible. (1 = trachea, 2 = heart, 3 = lungs, 4 = liver, asterisks = sternotracheal muscles, arrows = tracheolateral muscles) Adapted from Casteleyn et al. (2011a)

Fig. 12. Left craniolateral view of the cranial thoracic aperture of a goose demonstrating the tracheal elongation that is visible as a ventral loop. Adapted from Casteleyn et al. (2011a)
Fig. 13. Ventral view of the chicken syrinx (boxed) that is located in between the trachea (1) and the left and right primary bronchi (2 and 2’, respectively). The sternotracheal muscles are indicated by the asterisks. Adapted from Casteleyn et al. (2011a).

Fig. 14. A: Longitudinal histologic section of the syrinx of a chicken (after Casteleyn et al., 2011a). B: Schematic representation of the syrinx of the blackbird (*Turdus merula*) adapted from King (1979) and Vollmerhaus and Sinowatz (1992). (1 = trachea, 2 = *Tymannum*, 3 = *Pessulus*, 4 = medial *Labia*, 5 = lateral tympaniform membranes, 6 = lateral *Labia*, 7 = medial tympaniform membranes, 8 = interbronchial ligament, 9 = primary bronchi, asterisks = sternotracheal muscles)

Fig. 15. Ventral view of the syrinx of a drake located in between the trachea (1) and the left and right primary bronchi (2 and 2’, respectively). The sternotracheal muscles are indicated by the asterisks. The syringeal bulla (3) is clearly visible as a voluminous extension at the left side of the syrinx. Adapted from Casteleyn et al. (2011a).

Fig. 16. Ventral view of the trachea of a pigeon showing the left and right sternotracheal muscle (1 and 1’, respectively) and the left and right tracheolateral muscles (2 and 2’, respectively). The syrinx (boxed) is located at the tracheal bifurcation. Adapted from Casteleyn et al. (2011b)
Fig. 11

Fig. 12