



Coos, booms, and hoots: The evolution of closed-mouth vocal behavior in birds

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Most birds vocalize with an open beak, but vocalization with a closed beak into an inflating cavity occurs in territorial or courtship displays in disparate species throughout birds. Closed-mouth vocalizations generate resonance conditions that favor low-frequency sounds. By contrast, open-mouth vocalizations cover a wider frequency range. Here we describe closed-mouth vocalizations of birds from functional and morphological perspectives and assess the distribution of closed-mouth vocalizations in birds and related outgroups. Ancestral-state optimizations of body size and vocal behavior indicate that closed-mouth vocalizations are unlikely to be ancestral in birds and have evolved independently at least 16 times within Aves, predominantly in large-bodied lineages. Closed-mouth vocalizations are rare in the small-bodied passerines. In light of these results and body size trends in nonavian dinosaurs, we suggest that the capacity for closed-mouth vocalization was present in at least some extinct nonavian dinosaurs. As in birds, this behavior may have been limited to sexually selected vocal displays, and hence would have co-occurred with open-mouthed vocalizations.

KEY WORDS: Bioacoustics, hyoid skeleton, motor pattern, tongue, vocal production.

Vocal signals are important in the communication systems of animals, particularly insects, anurans, mammals, and birds (Catchpole and Slater 2008; Bradbury and Vehrencamp 2011). In songbirds, hummingbirds, parrots, and some suboscines, vocal characteristics are acquired through a complex learning process (Zeigler and Marler 2008). For the normal expression of these signals, the central nervous system coordinates a sound source, the syrinx, and a vocal-tract filter. Syringeal anatomy and function have received attention for more than 150 years (Müller 1847; King 1989; Elemans 2014), but the importance of movements of the vocal tract (e.g., trachea, larynx, oropharyngeal-esophageal cavity, beak) to vocal production in many groups was recognized only recently (Hersch 1966; Nowicki 1987; Goller et al. 2004; Podos et al. 2004). Moreover, neither interspecific variation nor evolution of vocal-tract dynamics has been studied explicitly.

Most birds vocalize with the beak open, accompanied by conspicuous and complex movements of the neck and beak (Westneat

et al. 1993; Goller et al. 2004; Daley and Goller 2004; Podos et al. 2004; Riede et al. 2006, 2013; Ohms et al. 2012; Derryberry et al. 2012). These movements are a dynamic component of upper-vocal-tract filtering (Riede and Goller 2010). Another vocalization pattern is to seal off the pharyngeal from the oral and nasal cavity and to inflate an internal structure in the ventral neck area, between the beak and thoracic aperture. This phonatory mechanism has been studied in only a handful of bird species, including the domesticated ringed turtle-dove (*Streptopelia risoria*; Riede et al. 2004) and greater sage-grouse (*Centrocercus urophasianus*; Krakauer et al. 2009; species names of wild birds follow Gill and Donsker 2015). However, the phylogenetic distribution and evolutionary origin(s) of closed-mouth vocalizations have not been studied (Dantzker and Bradbury 2006).

We use the term “closed-mouth vocalization” for vocal behavior with a closed beak and the simultaneous inflation of the esophagus or tracheal pouches. We recognize that, unlike many

mammals possessing soft tissue lips, a closed beak alone is not sufficient to reroute air into an inflatable structure. Vocal behavior with a narrow beak gape is well known (Riede et al. 2006) but a distinct vocal behavior. For example, whisper songs in passerines (Reichard and Welkin 2015; e.g., in corvids; Goodwin 1986; Webber and Stefani 1990), are often produced with an almost closed beak. However, the acoustic filter effect of this narrow beak gape can be predicted using an open-mouth model as sound radiated from a small opening (Fletcher et al. 2006). As explained below, the acoustic effects of closed-mouth vocalization are fundamentally different, with potential effects on the sound source and the vocal tract filter. We therefore classify all vocal behavior with the beak open and therefore not associated with the inflation of a flexible cavity as “open-mouth vocalization,” even if the beak gape is very slight.

Both open- and closed-mouth vocalizations occur in extant archosaurs (birds, crocodiles), as well as in other reptiles (in Testudines and Lepidosauria; Britton 2001; Sacchi et al. 2004). Although comparatively widespread, vocal behavior in nonavian reptiles is often perceived to be less common than in birds, perhaps because acoustic signaling in nonavian reptiles occurs predominantly over short distances, and hence is relatively inconspicuous to human observers (Gans and Maderson 1973; Vergne et al. 2009).

Here, we investigate (i) the phylogenetic distribution of closed-mouth vocalizations in Aves and nonavian reptile outgroups, and (ii) whether open- or closed-mouth vocalizations in sexual displays were ancestral within Aves. We present the first detailed review of morphological and biomechanical properties of closed-mouth vocalizations in birds, and identify acoustic correlates of this behavior. Based on these data and ancestral-state reconstructions of the mode of upper-vocal-tract filtering, we discuss its estimated evolutionary origins, and ask what life history or other attributes may explain its phylogenetic distribution.

MORPHOLOGICAL AND BIOMECHANICAL ASPECTS OF INFLATION OF THE VENTRAL NECK REGION DURING CLOSED-MOUTH VOCALIZATIONS

Most simply, inflation of a vocal sac during closed-mouth vocalizations requires rerouting of exhaled respiratory air and a morphological structure that can receive this air. Physiology of inflation has been studied directly only in doves (Riede et al. 2004), but behavioral observations suggest that the basic respiratory mechanism is similar for both open- and closed-mouth vocalizations in birds (Hartley and Suthers 1989; Goller and Suthers 1996, 1999; Wild et al. 1998). Birds typically (but not exclusively) vocalize during expiration (Hartley and Suthers 1989; Goller and Suthers 1996, 1999; Wild et al. 1998) but, in taxa with a vocal sac, the beak and nares are closed to allow expiratory air to move into the inflatable cavity rather than to exit through the

mouth or nasal openings. For example, before doves start to coo, inspiration is followed by a closing of the beak and nares, and expiratory air then flows into the esophagus. These prephonatory movements begin to inflate the esophagus, then the bird starts cooing with the vocal organ, the syrinx (Riede et al. 2004). During each call the bird expires into the esophagus while the beak is closed, and between calls the beak is opened for inspiration. During the interval between calls, the esophagus partly deflates, making room for the volume of air to be expired during the next call. The tracheal tube plays an important role as the first part of the vocal-tract filter. The inflated sac facilitates the subsequent filter effect, which is affected by the degree of inflation only moderately. Ultimately, sound is radiated from the inflated sac and overlying skin, as demonstrated by computational simulation (Fletcher et al. 2004), by a physical model (Riede et al. 2008), and by acoustic analysis of calls in ringed turtle-doves (Beckers et al. 2003) and pectoral sandpipers (*Calidris melanotos*; Riede et al. 2015). No direct measurements of the characteristics of the vibrating neck skin or sound-radiation patterns have been made for any bird or crocodylians. Furthermore, there is no evidence to date that call duration or mini-breath production are affected by closed-mouth vocalization.

In most closed-mouth vocal behavior in birds, expired air inflates the distensible esophagus or a sac derived from the upper esophagus (Table S3). Knowledge of this mechanism is based primarily on morphological studies (Table S3), but was confirmed by morphological and cineradiographic analysis in ringed turtle-doves (Riede et al. 2004). The avian esophagus is composed entirely of smooth musculature (Ingelfinger 1958; Geyikoğlu et al. 2002), which allows for extensive expansion of its wall. In contrast, gular pouches branch off from the upper esophagus. They represent an extension of the pharynx, and can extend below the tongue and between the branches of the mandible. Gular pouches are found in many species in which they are used for food storage and transport, for thermoregulation and, possibly, as an optical signal, but not for vocalization—e.g., in Alcidae (Speich and Manuwal 1974), Pelecanidae (Bartholomew et al. 1968), and Threskiornithidae (Rudegeair 1975). The gular pouch also should not be confused with the crop; the latter is the lower part of the esophagus separated from the upper esophagus by ring musculature. In ringed turtle-doves, the crop is not inflated during vocalization (Riede et al. 2004).

Intraesophageal pressure measurements in ringed turtle-doves revealed an increase in pressure up to 0.5 kPa beyond ambient pressure during closed-mouth vocalization (Riede et al. 2004), but the mechanism of how the upper respiratory tract is sealed has not been investigated. Several possible nonexclusive mechanisms for creating a tight seal exist, for example pressing together the upper and lower mandibles, or pushing the tongue against the hard palate. The bony cornua of the hyoid

skeleton (epibrachiale and ceratobrachiale), and muscles attaching to these elements, likely contribute to this seal laterally. This proposed mechanism is consistent with descriptions of the mobility of the avian tongue and hyoid skeleton during feeding (Zweers et al. 1981), and during vocalization in songbirds (Suthers et al. 2015). The larynx cannot be involved because the glottis must be open to release the expired air into the esophagus.

In species that inflate an evagination of the trachea instead of the esophagus, it is likely that the glottal valve is closed to avoid movement of air into the oral, pharyngeal, and esophageal cavities (McLelland 1989). The best known examples of birds utilizing a flexible tracheal structure are the emu (*Dromaius novaehollandiae*) and ruddy duck (*Oxyura jamaicensis*; Murie 1867; Wetmore 1918; McLelland 1989). The trachea in the emu, for example, features 7–12 ventrally incomplete tracheal rings (Coughtrey 1873; Noble 1973) that form a cleft-like opening from the trachea into the sac. Increasing pressure inside the trachea above the syrinx causes the membranous sac to expand subcutaneously.

Male ducks (Anatidae) have tracheo-bronchial structures that form large, stiff cavities at or near the syrinx; these cavities range from solid noninflatable structures, to structures with fenestrae covered by flexible membranes, which presumably allow some inflation (Johnsgard 1961; King 1989; Miller et al. 2007; Pierko 2010).

Cranial and cervical air sacs (as part of “postcranial skeletal pneumatization”) have been described in many extant birds (Duncker 1971; Bezuidenhout et al. 1999; Maina 2005) and were common in nonavian dinosaurs (Martin and Palmer 2014; Brusatte et al. 2015). Correlates of air sacs also have been identified in extinct avian outgroups (O’Conner 2009; Wedel 2009; Benson et al. 2012). These air sacs do not appear to play a specific role as resonating structures in closed-beak vocalization. Neither the tracheal sac of emus, nor the inflatable esophagus in Columbiformes (ringed turtle-dove; rock dove, *Columba livia*), Charadriiformes (pectoral sandpiper), or Galliformes (greater sage-grouse) have a connection between the respective inflatable cavity and the air-sac system. Furthermore, cineradiography confirmed that inflation of cervical air sacs does not occur during vocalization in ringed turtle-doves (Riede et al. 2004), in the open-mouth vocalizing species monk parakeet (*Myiopsitta monachus*; Ohms et al. 2012), or in the open-mouth vocalizations of songbirds (Riede and Suthers 2009; Ohms et al. 2010; Riede and Goller 2010; Riede et al. 2013).

ACOUSTIC PROPERTIES OF CLOSED-MOUTH VOCALIZATION

The acoustic effect of inflation of the esophagus or tracheal pouch is similar across avian taxa. The acoustic features of hooting calls (e.g., pectoral sandpiper), coo calls (e.g., ringed turtle-dove, rock dove), and booming calls (e.g., rhea, cassowaries *Casuaris* spp.,

Eurasian bittern *Botaurus stellaris*, houbara bustard *Chlamydotis undulata*) all demonstrate a periodic source signal with a comparatively low fundamental frequency (F_0) (Slabbekoorn et al. 1999; Puglisi et al. 2001; Mack and Jones 2003; Cornec et al. 2014, 2015). The effect is exemplified with a dove coo call (Fig. 1). In the case of the ring dove, there is little detectable energy in higher harmonics. The acoustic signal generated at the syrinx is strongly filtered, and only a small band of acoustic energy is eventually radiated from the ventral neck area. The low amplitude or absence of higher harmonics in sounds with low fundamental frequency emitted with a closed-mouth mechanism may result from the low-pass filter characteristic of the esophagus wall and overlying skin (Fletcher et al. 2004).

In closed-mouth vocalizations there is only one major resonance frequency, which is tuned to one harmonic of the source signal (Fletcher et al. 2004). Open-mouth vocalizations facilitate more complex resonance acoustics: more than one resonance frequency can be present, depending simply on the length and shape of the oropharyngeal-esophageal cavity (OEC; Fletcher et al. 2006). The positions of resonance frequencies can also be dynamically altered during open-mouth vocalizing in birds (Riede et al. 2006, 2013). Through movements of the hyoid skeleton, tongue, and open beak, only open-mouth vocalization birds are able to dynamically alter OEC shape (Riede et al. 2006, 2013; Suthers et al. 2015). Communicative functions of multiple resonances in the vocal repertoire are unknown, but the ability of birds to produce and perceive multiple resonances is demonstrated by their ability to imitate human speech, in which a minimum of two resonances is required to produce different vowels (Stevens 2000). This flexibility is not possible in closed-beak vocalization.

Vocalization into an inflatable cavity can produce lower frequencies than vocalization into an open and tube-like vocal tract of similar size (Riede et al. 2008). Two mechanisms, which need to be supported further by empirical data in avian models, could facilitate the link between closed-mouth vocalization and the production of low- F_0 vocalizations: (a) better power radiation in the low frequency range; and (b) if the resonance cavity affects dynamics of the vibrating tissues of the syrinx (i.e., a nonlinear feedback mechanism between sound source and vocal-tract filter; Titze et al. 2008). The inflated cavity (esophagus or tracheal pouch) would function as an impedance-matching device, whereby sound radiation through the skin of the neck generates a strong filtering effect, that is the stretched skin acts as a band-pass filter eliminating higher and lower spectral energy (Fletcher et al. 2004).

Goller and Riede (2013) outlined four variables that determine the F_0 range for bird vocalizations: size and shape of the vibrating tissue; mechanical properties of the vibrating tissue; lung pressure; and interactions between sound source and vocal tract. F_0 range is related to body size, through size-dependent

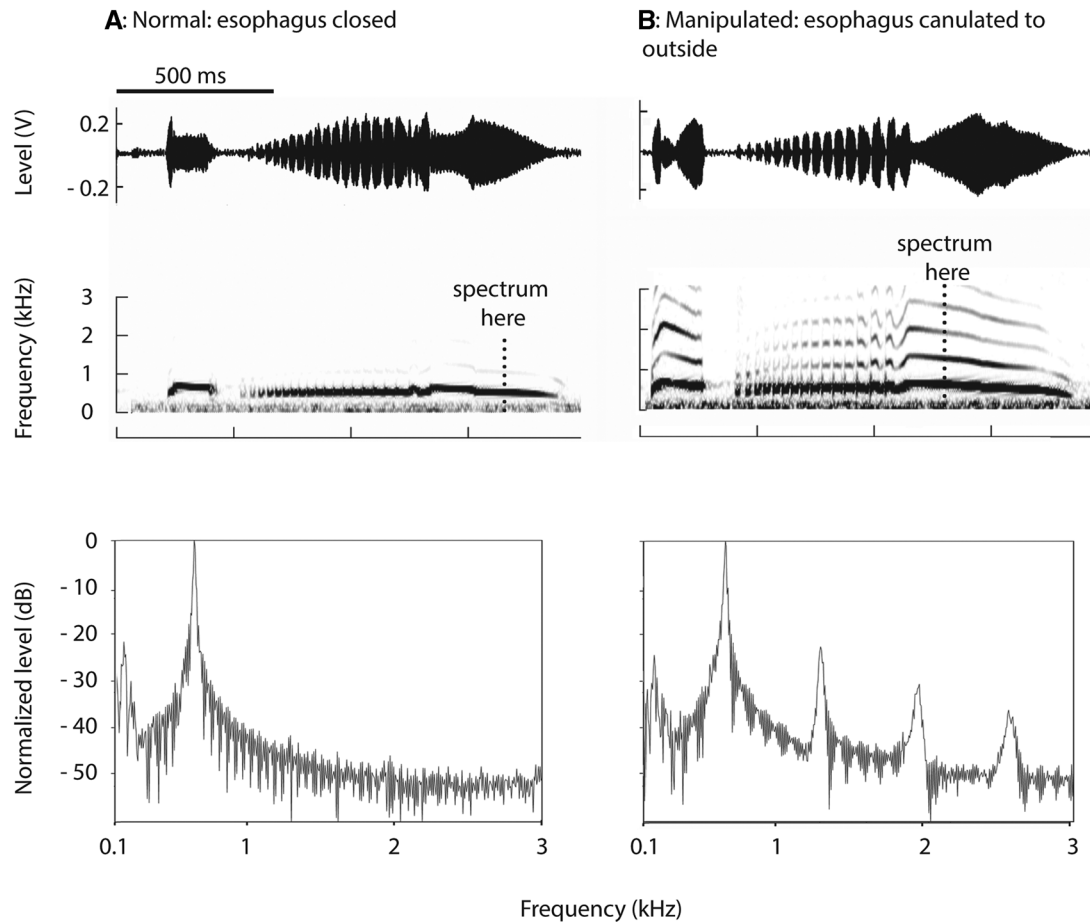


Figure 1. The inflated esophagus of doves and pigeons filters high frequencies of syringeally produced calls during closed-beak vocal behaviors. (A) Normal *coo* call, with esophagus closed to outside. (B) Call produced when the esophagus is open to outside air through a cannula. The calls were uttered by a single male ring dove (*Streptopelia risoria*). From top to bottom: oscillograms (amplitude, relative change in output voltage of microphone signal); sound spectrograms; and power spectra (after Riede et al. 2004). Power spectra (bottom panels) are derived from a 100-ms segment during the second half of the *coo*, centered on the time indicated by the dotted line in the spectrogram.

biomechanical constraints of the syringeal cartilage framework, and by viscoelastic constraints set by tension of the vibrating tissue. Here, we investigate the phylogenetic distribution of closed-mouth vocalization and its potential relationship with one of these variables, body size.

Methods

THE DISTRIBUTION OF CLOSED-MOUTH VOCALIZATIONS IN BIRDS

Closed-mouth vocalizations represent only part of the vocal repertoire of the taxa in which they are present. We collected data on open- and closed-mouth vocalizations that are used specifically in courtship or territorial displays. Other calls in the vocal repertoire of birds (e.g., during begging by chicks; in aggressive encounters) typically are open-mouth vocalizations (Kilner 1997; Saino et al. 2008). Indeed, there are no described avian calls utilizing

closed-mouth vocalization in other contexts, but data for many species remain limited. Information on closed-mouth vocalizations came from: (a) published studies on individual species describing neck enlargement while the beak remained closed during vocalization; and (b) online publicly available videos. In total, our dataset included vocalization behavior for 208 bird species (Gill and Donsker 2015) and four outgroup species (Table S4). *F0*-estimates for a selected group of closed-mouth vocalizers also were plotted against body mass, and contrasted graphically with the predicted general relationship between upper and lower *F0* boundaries (Fig. 2; Goller and Riede 2013).

ANCESTRAL STATE RECONSTRUCTION OF CLOSED-MOUTH/BEAK VOCAL BEHAVIOR

We plotted the distribution of closed-mouth vocalizations on the recent avian supertree of Burleigh et al. (2015) and on a set of 500 time-calibrated trees from Jetz et al. (2012). The tree of Burleigh

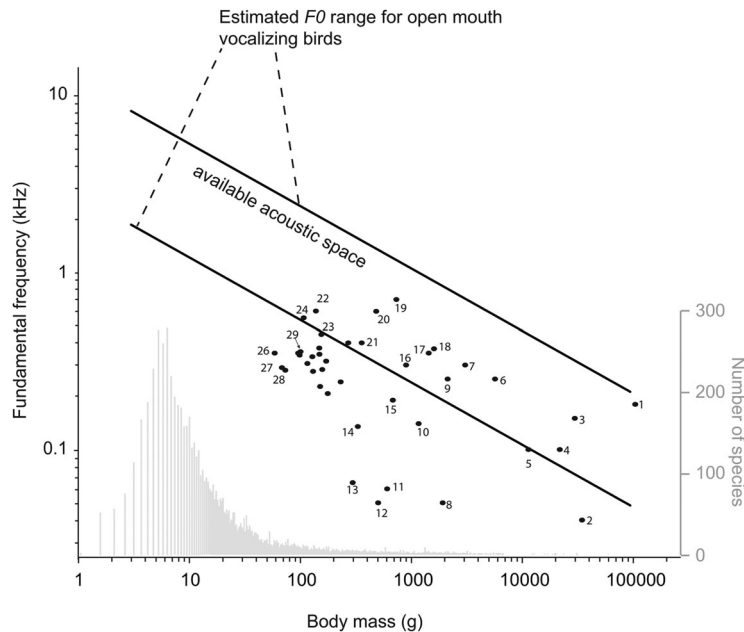


Figure 2. Fundamental frequency (F_0) of vocalizations in birds that vocalize with the mouth closed (closed-mouth vocalization species) is lower than predicted from body size alone. The two black lines indicate the estimated lower and upper boundaries for F_0 range based on body size. The area between the two lines approximates the “available acoustic space” for vocalizing birds, and was estimated based on a simplified string model of the syringeal sound source and a linear source-filter theory (after Goller and Riede 2013). The fundamental frequencies of vocalizations by closed-mouth vocalization species (dots; Table S3) are close to or below the lower boundary. Gray bars and secondary y-axis: avian body mass distribution (data from Dunning 2008; Table S3). Key: 1, ostrich *Struthio camelus*; 2, northern cassowary *Casuarius unappendiculatus*; 3, emu *Dromaius novaehollandiae*; 4, greater rhea *Rhea americana*; 5, great bustard *Otis tarda*; 6, Australian bustard *Ardeotis australis*; 7, sage grouse *Centrocercus urophasianus*; 8, kakapo *Strigops habroptilus*; 9, common eider *Somateria mollissima*; 10, great bittern *Botaurus stellaris*; 11, ruddy duck *Oxyura jamaicensis*; 12, rock ptarmigan *Lagopus muta*; 13, Eurasian woodcock *Scolopax rusticola*; 14, capuchinbird *Perissocephalus tricolor*; 15, American bittern *Botaurus lentiginosus*; 16, greater prairie chicken *Tympanuchus cupido*; 17, speckled eider *Somateria fischeri*; 18, king eider *Somateria spectabilis*; 19, lesser prairie chicken *Tympanuchus pallidicinctus*; 20, pheasant pigeon *Otidiphaps nobilis*; 21, rock pigeon *Columba livia*; 22, *Streptopelia capicola*; 23, *Streptopelia chinensis*; 24, *Streptopelia vinacea*; 25, capuchinbird *Perissocephalus tricolor*; 26, small buttonquail *Turnix sylvaticus*; 27, little buttonquail *Turnix velox*; 28, painted buttonquail, *Turnix varius*; 29, pectoral sandpiper *Calidris melanotos*; Unlabeled dots include several *Streptopelia* species: *St. bitorqua*, *St. decaocto*, *St. turtur*, *St. semitorquata*, *St. hypopyrrha*, *St. orientalis*, *St. lugens*, *St. picturata*, *St. senegalensis*, *St. tranquebarica*.

et al. (2015) provided branch lengths in units of proportional genetic change and not time, so we used the congruification package in R (Eastman et al. 2013) to calibrate the nodes of the tree according to a recent time-calibrated phylogenetic tree inferred from genomic data (Jarvis et al. 2014). We then estimated branch lengths using penalized likelihood in the treePL program (Smith and O’Meara 2012). We used a random cross-validation procedure to arrive at the best estimate of the smoothing parameter (0.01). Species not represented in Burleigh et al. (2015) or Jetz et al. (2012) were added to the most inclusive genera with the add.species.to.genus function in the phytools R package (Revell 2011). We grafted outgroups to the tree with the bind.tip function in phytools based on published divergence-time estimates (Hedges et al. 2015).

To reconstruct ancestral states, we used a maximum likelihood approach implemented in the rayDISC function in the

corHMM package (Beaulieu et al. 2013). We chose this method because it allows for polytomies. We compared the fit of three different models of character evolution using the pruned tree of Burleigh et al. (2015): (a) an equal rates model in which instantaneous character change between open- and closed-mouth vocalization is equivalent; (b) a model in which transitions from between states are asymmetrical (all rates different); and (c) an equal rates model that allows for different transition rates in different parts of the phylogeny (i.e., a hidden Markov model implemented in the corHMM package). We used AICc to select the best model. Our final dataset included evidence of vocalization behavior for 208 out of ~10,500 (Gill and Donsker 2015) bird species. We therefore explored how incomplete taxon sampling, along with phylogenetic uncertainty, might influence our ancestral state reconstructions using simulations and alternative phylogenies (see Supplementary Methods and Results).

THE RELATIONSHIP BETWEEN VOCAL BEHAVIOR AND BODY SIZE

To test for a relationship between mode of vocal production and body size, we used phylogenetic logistic regression in the *phylolm* package (Ho and Ané 2014). We chose this approach because vocal behavior (i.e., open- vs. closed-mouth vocalization), the response variable, is binary and not continuous, and because it allowed us to estimate regression parameters and phylogenetic signal (α parameter) simultaneously. Following Ives and Garland (2010), we used parametric bootstrapping ($n = 2000$ replicates) and assessed statistical significance based on whether the 95% confidence intervals for estimates (slope, intercept) overlapped zero.

To investigate whether an increase in body size preceded, arose coincident with, or followed the origin of closed-mouth vocalization, we reconstructed ancestral states of body size. To define size classes, we used k-means clustering (Hartigan and Wong 1979) on natural-log-transformed body masses from a large dataset (Dunning 2008). This resulted in a cutoff of ~ 100 g between small and large birds. To test whether the evolution of closed-mouth vocalization was more likely to occur in large-bodied lineages, we performed a concentrated changes test (CCT; Maddison 1990) in *Macclade* v.4 (Maddison and Maddison 1992). Briefly, we randomly resolved all polytomies and reconstructed ancestral states of body-size using unordered parsimony under ACCTRAN and DELTRAN optimizations. We then ran 5000 simulations to determine the null distribution for gains of closed-mouth vocalization in large-bodied lineages, as the large number of changes in vocalization behavior prohibited the use of the exact CCT algorithm described by Maddison (1990). We also tested whether gains of closed-mouth vocalization occurred more often in large-bodied lineages using a contingent states test (Supplemental Methods and Results, Table S2).

Results

THE DISTRIBUTION OF CLOSED-MOUTH VOCALIZATION IN BIRDS

We identified 16 origins of closed-mouth vocalization. Fifty-two bird species from 16 traditionally recognized families vocalize with neck expansion while the beak remains closed (Table S3). Both expanded neck and closed beak were used as signs of vocalizing into an inflating or inflated cavity (i.e., closed-mouth vocalization). Fundamental frequencies of closed-mouth vocalization species were confined to the lower boundary of predicted frequencies based on body size alone. Most closed-mouth vocalizers were larger than 100 g in body mass (Fig. 2). Closed-mouth vocalizers range in body mass from 37 g to 110 kg, but only 4 of the 52 bird species weigh less than 100 g (Table S3).

ANCESTRAL STATE RECONSTRUCTION AND REPEATED EVOLUTION OF CLOSED-MOUTH VOCALIZATION IN BIRDS

The best-fitting evolutionary model for the evolution of vocal behavior was the equal rates model ($AIC_C = 107.12$), but the model with different rates of gain and loss of closed-mouth vocalization also received moderate support ($AIC_C = 108.91$, alternative model ($\Delta AIC_C < 2$); see Gelman and Hill 2007). The hidden rates model received lowest support ($\Delta AIC_C = 5.39$). Under the best-fitting equal rates model, open-mouth vocalization was likely the ancestral avian vocal mechanism in Aves ($P(\text{open mouth}) = 0.88$, $\Delta AIC_C = 4.00$). The ancestral neognath was likely an open-beak vocalizer ($P(\text{open mouth}) > 0.99$; ΔAIC_C alternative model = 20.57), but the ancestral state of palaeognaths was ambiguous ($P(\text{open mouth}) = 0.75$, ΔAIC_C alternative = 2.25; Fig. 3). This analysis recovered at least 16 gains of closed-mouth vocalization in Archosauria and one loss in Aves (greater painted-snipe, *Rostratula benghalensis*).

Sensitivity analyses showed that the ancestral state of vocalization behavior in Paleognathae was more sensitive to taxon sampling and phylogeny than that for Aves and Neognathae (see Fig. S1). Using alternative phylogenies for ancestral state reconstruction yielded similar results for the neognath ancestor, but Aves and Palaeognathae were estimated as slightly more likely to have had closed-mouth vocalization ancestrally (Supplementary Methods and Results, Fig. S2). However, in no cases did closed-mouth vocalization become the more likely ancestral state at these nodes even when $\sim 50\%$ of unsampled Aves, mostly passerines were assigned this state (Supplementary Methods and Results, Fig. S1).

CLOSED-MOUTH VOCALIZATION EVOLVES MORE FREQUENTLY IN LARGE-BODIED LINEAGES

Ancestral state reconstructions using discrete body sizes ($n = 211$ species) revealed that the evolution of closed-mouth vocalization in birds was preceded by the evolution of large (> 100 g) body size (Fig. S4). Closed-mouth vocalization was more likely to evolve in large-bodied lineages (concentrated changes test, $P < 0.001$ for both ACCTRAN and DELTRAN optimizations). Contingent states tests showed that ancestral body sizes estimated from a much larger dataset (5576 species from Dunning 2008) did not influence the results recovered with the pruned 211 taxon phylogeny, that is that closed-mouth vocalization is more likely to occur in large-bodied lineages (see Supplementary Methods and Results, Table S2). However, we found no evidence for correlated evolution of vocal behavior and discrete body size categories ($\Delta AIC_C = 5.33$ relative to the simpler model of independent trait evolution); large species were not significantly more likely than small species to use closed-mouth vocalizations (Table S1, Fig. S3).

Discussion

Our analyses suggest that open-mouth vocalization likely was ancestral to crown Aves. Closed-mouth vocalization evolved at least 16 times in Archosauria (Fig. 3), and in all cases was preceded by an increase in body size (Fig. S4). The one loss of closed-mouth vocalization (in painted-snipes) was not associated with a change in body size (Fig. S4). Aves is nested within theropod dinosaurs, which show a wide range of body sizes (many Mesozoic birds exceeded 1000 g in body mass) as well as many independent increases in body size within distinct clades closely related to birds (Turner et al. 2007; Benson et al. 2014; Lee et al. 2014). The implications of our results for the evolution of vocal behavior in archosaurs including extinct forms are explored below.

SELECTIVE CONDITIONS THAT MAY FAVOR THE EVOLUTION OF CLOSED-MOUTH VOCALIZATION

Closed-mouth vocalization is associated with low fundamental frequencies in birds (Fig. 2). In species that employ both mechanisms (recordings were available for Greater Sage-grouse and Pectoral Sandpiper), closed-mouth vocalizations are lower in fundamental frequency than open-mouth vocalizations. However, there are alternative mechanisms for producing low-frequency sounds, including an enlarged syrinx (King 1989), specialization of two syringeal sound sources for high and low frequencies (Suthers 1990), and tracheal elongation (Gaunt et al. 1987; Fitch 1999). Interestingly, closed-mouth vocalization is apparently absent in species with tracheal elongation (Fig. 3); therefore, why does closed-mouth vocalization evolve? Below we discuss potential relationships to mating system and female preference, sound propagation, and multimodal signaling. Biomechanical and motor control aspects are discussed in the subsequent two sections.

Species showing closed-mouth vocalization are relatively large and use low-frequency sounds during courtship (Fig. 2). Apart from a few exceptions (e.g., emu; Halkin and Evans 1999a, b), closed-mouth vocalization is employed by advertising males. In cassowaries, females produce sounds with a very low fundamental frequency, but it is unknown if they employ the same closed-mouth mechanism as males. Although few data on female preference exist, low frequency calls may evolve by sexual selection if low fundamental frequency calls indicate quality-related information (Cornec et al. 2015; Freeman and Hare 2015) that is favored through mate choice (Riebel 2009). Interestingly, it appears that no particular mating system is associated with closed-mouth vocalization: among closed-mouth vocalizers are polygynous lek breeders without paternal care (e.g., Greater Sage-grouse), polygamous species with paternal care (e.g., Rhea), as well as socially monogamous species with high levels of pater-

nal care (e.g., Columbiformes; Cassowary; Emu; Handford and Mares 1985).

Features related to fundamental frequency, such as range, minimum, maximum, or modulation rate, can also improve sound transmission in certain environments and increase communication distance (Cosens and Falls 1984; Garstang et al. 1995; Slabbekoorn and ten Cate 1996; Seddon 2005; Boncoraglio and Nicola 2007). Beyond the basic necessity to radiate sound, specific radiation patterns could be advantageous by being directed at particular receivers (Dantzker et al. 1999). During closed-mouth vocalization, low-frequency sound is radiated from the skin overlying the inflated esophagus or tracheal pouch. Feather-free skin, either on the entire neck (e.g., ostrich; frigatebird) or as lateral areas (e.g., grouse; prairie chicken), can generate specific radiation patterns around the vocalizing animal (Dantzker et al. 1999).

Rhythmic neck expansion could also serve to propagate an optical signal (Cooper and Goller 2004). Closed-mouth vocalizations sometimes are combined with elaborate skin color or movement to produce a conspicuous visual signal in birds (Dantzker et al. 1999; Madsen et al. 2004) and other groups (Starnberger et al. 2014). For example, the two sibling-species, Dusky Grouse (*Dendragapus obscurus*) and Sooty Grouse (*D. fuliginosus*), are both closed-mouth vocalizers and show prominent dark red and yellow lateral skin areas, respectively (Brooks 1929). Furthermore, movements around the time of sound production include head and neck movements in eiders *Somateria* spp. (Johnsgard 1964), head movements in common wood pigeon *Columba palumbus* (Murton and Isaacson 1962), and fluttering of the bright red neck skin in frigatebirds (*Fregata* spp.; both open- and closed-mouth vocalizations occur in *Fregata*). Movements before or during vocalization presumably have signal function even in species that lack striking markings (e.g., pectoral sandpiper; Riede et al. 2015).

BIOMECHANICAL ASPECTS OF CLOSED-MOUTH VOCALIZATIONS

The main mechanical challenge to production of closed-mouth vocalizations in many species is expanding the esophagus to accept expired air. Esophageal inflation is facilitated by two important features. First, the pharynx and upper esophagus in birds, nonavian reptiles and most amphibians is expandable, perhaps associated with the widespread ability in the clade to swallow large prey items. In birds (unlike mammals) an upper esophageal sphincter is absent, which permits substantial expansion of the oro-pharyngeal area. Second, the esophagus is composed entirely of smooth musculature in amphibians, nonavian reptiles, and birds (Ingelfinger 1958; Yoshida 2001; Geyikoglu et al. 2002; Uriona et al. 2005), which allows more expansion than is possible in mammals, where the esophageal musculature comprises both smooth and striated musculature (Meyer et al. 1986; Patapoutian

et al. 1995). The latter muscle type is much less pliable and therefore prevents expansion. However, the skin of the ventral neck needs to be sufficiently elastic or loose to permit expansion of the esophagus or other inflatable structures. In the rock dove (Baumel et al. 1983) and pectoral sandpiper (Riede et al. 2015), the overlying skin contains fat embedded in a loose net of connective tissue. In the American alligator *Alligator mississippiensis*, the alternation between stiff scales and highly elastic skin between scales enables the ventral neck area to be stretched (Hopkins-Dubansky 2012).

Our analysis suggests a relationship of closed-mouth vocalization to body size in the evolution in birds. First, closed-mouth vocalization is used by species > 100 g in body mass; and second, the origin of closed-mouth vocalization was always preceded by an increase in body size (Fig. 3). The inflation of an elastic cavity could present a size-dependent challenge. The lung pressure required to do this depends on the tension in the wall of the inflatable cavity divided by the radius of curvature of the surface. The viscoelastic properties of soft tissue are nonlinear, that is tension does not increase in proportion to radius. Thus, for the same tension, the pressure is greater when the radius is small, which may be why closed-beak vocalization is not found among small species.

LABILE EVOLUTION OF CLOSED-MOUTH VOCALIZATION IN TETRAPODS

The two main filter mechanisms for enhancing low-frequency vocalizations are tracheal elongation and closed-mouth vocalization; the latter is a dynamic mechanism that allows transient use of resonance control. For example, pectoral sandpipers use both open- and closed-mouth vocalization during their lek displays (Riede et al. 2015). In contrast, tracheal elongation uses a fixed tracheal resonance and faces possible physiological consequences of enlarged dead space. Future studies will have to further explore how morphological and physiological features, such as body size or respiratory demands, are linked to acoustic traits (e.g., Mason and Burns 2015) or anatomical features of the syrinx and vocal tract, and thereby may have influenced their evolution. Furthermore, the generation of low fundamental frequencies requires adaptations of both the sound source (e.g., sexual dimorphism of the syrinx; bipartite syrinx) and upper-vocal-tract filter mechanisms, and it remains to be seen if a specific sound source design dictates particular filter mechanism.

Open-mouth vocalizations are effective for sound-energy radiation, in particular in the upper frequency range, and allow for dynamic adjustment of resonance frequency, which facilitates vocalization over a broad frequency range. In particular, in the most species-rich order of extant birds (Passeriformes), open-mouth vocalization is the predominant mechanism (e.g., Podos et al. 2004; Derryberry et al. 2012); we only found one

passerine, the capuchinbird (*Perissocephalus tricolor*) that uses closed-mouth vocalizations. In that clade, open-mouth vocalization is associated with the ability for vocal learning (Zeigler and Marler 2008) and selection for song complexity (Riebel 2009). The ability to dynamically adjust upper-vocal-tract resonance frequencies facilitates the use of a broader range of frequencies within a species' repertoire, and thereby enables the evolution of acoustic complexity.

Open- and closed-mouth vocalizations also are present in other tetrapods. For example, some crocodylians (e.g., American alligator; Riede et al. 2011), the closest living relatives of birds, use both vocal behaviors in different contexts. Closed-mouth vocalizations are used in display and territorial calls (Britton 2001). Some mammals use both, open- and closed-mouth vocalization (e.g., siamang *Symphalangus syndactylus*; Riede et al. 2008), and both vocal modes occur in Lissamphibia, with closed-mouth vocalizations used for mate advertisement and open-mouth vocalizations for distress calls in some anurans (Gridi-Papp 2008).

CLOSED-MOUTH VOCALIZATION IN VERTEBRATES LIKELY IS BASED ON A CONSERVED MOTOR PATTERN

The evolution of open- and closed-mouth vocalization touches on a central question in neuroethology: how do complex behaviors evolve (Katz 2012)? We found independent repeated evolution of closed-mouth vocalization in Archosauria (Fig. 3), which may have been facilitated by a common mechanism of neuronal control that arose early in tetrapod evolution for respiratory control (i.e., buccal pumping; Bass et al. 2008), and for mastication and swallowing (Jean 2001; Luschei and Goldberg 1981).

The neuromuscular complex that regulates mandibular, hyoid, and laryngeal movements constitutes a feature of early tetrapods (Bass et al. 2008) and is used in display behavior in frogs (Schmidt 1966; Ryan and Guerra 2014) and nonavian reptiles (Font and Rome 1990; Wade 1998). However, both open- and closed-mouth vocalization require different but equally precise coordination of the mandible, hyoid skeleton, and larynx with respiratory movements, and how this coordination may occur is not understood. The repeated evolution of closed-mouth vocalizations suggests that the neural motor program for controlling hyomandibular structures has not only been maintained, but may be easily integrated into the vocal control mechanisms.

Closed-mouth vocalization functions with both laryngeal and syringeal sound sources and is present in amphibians, nonavian reptiles, and birds. American alligators produce territorial calls with the larynx, and appear to close off the laryngeal-pharyngeal area via the hyoid flap (Ferguson 1981; Reese 1945). During mating calls and juvenile contact calls, the ventral neck area expands (Britton 2001), suggesting inflation, but this possibility

needs to be confirmed with direct measurements of esophageal pressure. American alligators produce “alarm” calls with an open mouth (e.g., when a human approaches). In light of their lineage diversity and reconstructed repeated increases in body mass in lineages closely related to birds (e.g., Turner et al. 2007) and the recovered ambiguous ancestral state of vocalization behavior in the basal archosaur node (Fig. 3), it seems likely that both open- and closed-mouth vocalizations were present in nonavian dinosaurs. Following the pattern within extant tetrapods, closed-mouth vocalization may also have been limited to display or sexually selected vocal behaviors in dinosaurs and may be expected to show a relationship with reconstructed increases in body size.

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LITERATURE CITED

- Bartholomew, G. A., R. C. Lasiewski, and E. C. Crawford Jr. 1968. Patterns of panting and gular flutter in cormorants, pelicans, owls, and doves. *Condor* 70:31–34.
- Bass, A. H., E. H. Gilland, and R. Baker. 2008. Evolutionary origins for social vocalization in a vertebrate hindbrain–spinal compartment. *Science* 321:417–421.
- Baumel, J. J., A. F. Dalley, and T. H. Quinn. 1983. The collar plexus of subcutaneous thermoregulatory veins in the pigeon, *Columba livia*; its association with esophageal pulsation and gular flutter. *Zoomorphology* 102:215–239.
- Beaulieu, J. M., B. C. O’Meara, and M. J. Donoghue. 2013. Identifying hidden rate changes in the evolution of a binary morphological character: the evolution of plant habit in campanulid angiosperms. *Syst. Biol.* 62:725–737.
- Beckers, G. J. L., R. A. Suthers, and C. ten Cate. 2003. Mechanisms of frequency and amplitude modulation in ring dove song. *J. Exp. Biol.* 206:1833–1843.
- Benson, R. B. J., R. J. Butler, M. T. Carrano, and P. M. O’Connor. 2012. Air-filled postcranial bones in theropod dinosaurs: physiological implications and the ‘reptile’–bird transition. *Biol. Rev.* 87:168–193.
- Bezuidenhout, A. J., H. B. Groenewald, and J. T. Soley. 1999. An anatomical study of the respiratory air sacs in ostriches. *Onderstepoort J. Vet. Res.* 66:317–325.
- Boncoraglio, G., and N. Saino. 2007. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. *Funct. Ecol.* 21:134–142.
- Bradbury, J. W., and S. L. Vehrencamp. 2011. *Principles of Animal Communication*, 2nd ed. Sunderland MA: Sinauer Associates.
- Britton, A. R. C. 2001. Review and classification of call types of juvenile crocodylians and factors affecting distress calls. Pp. 364–377 in G. C. Grigg, F. Seebacher, and C. E. Franklin, eds. *Crocodylian Biology and Evolution*. Surrey Beatty & Sons, Chipping Norton, Australia.
- Brooks, A. 1929. On *Dendragapus obscurus obscurus*. *Auk* 46:111–113.
- Brusatte, S. L., J. K. O’Connor, and E. D. Jarvis. 2015. The origin and diversification of birds. *Curr. Biol.* 25:R888–R898.
- Burleigh, J. G., R. T. Kimball, and E. L. Braun. 2015. Building the avian tree of life using a large-scale, sparse supermatrix. *Mol. Phylogenet. Evol.* 84:53–63.
- Catchpole, C. K., and P. J. B. Slater. 2008. *Bird song: Biological themes and variations*, 2nd ed. Cambridge Univ. Press, Cambridge, UK.
- Cooper, B. G., and F. Goller. 2004. Multimodal signals: enhancement and constraint of song motor patterns by visual display. *Science* 303:544–546.
- Cornec, C., Y. Hingrat, and F. Rybak. 2014. Individual signature in a lekking species: visual and acoustic courtship parameters may help discriminating conspecifics in the houbara bustard. *Ethology* 120:1–12.
- Cornec, C., Y. Hingrat, A. Robert, A., and F. Rybak. 2015. The meaning of boom calls in a lekking bird: identity or quality information? *Anim. Behav.* 109:249–264.
- Cosens, S. E., and J. B. Falls. 1984. A comparison of sound propagation and song frequency in temperate marsh and grassland habitats. *Behav. Ecol. Sociobiol.* 15:161–170.
- Coughtrey, M. 1873. Note respecting the tracheal pouch of the emu. *Ann. Mag. Nat. Hist.* 12:217–218.
- Dantzker, M. S., and J. W. Bradbury. 2006. Vocal sacs and their role in avian acoustic display. *Acta Zool. Sinica* 52 (Suppl.):486–488.
- Dantzker, M. S., G. B. Deane, and J. W. Bradbury. 1999. Directional acoustic radiation in the strut display of male sage grouse *Centrocercus urophasianus*. *J. Exp. Biol.* 202:2893–2909.
- Daley, M., and F. Goller. 2004. Tracheal length changes during zebra finch song and their possible role in upper vocal tract filtering. *J. Neurobiol.* 59:319–330.
- Derryberry, E. P., N. Seddon, S. Claramunt, J. A. Tobias, A. Baker, A. Aleixo, and R. T. Brumfield. 2012. Correlated evolution of beak morphology and song in the neotropical woodcreeper radiation. *Evolution* 66:2784–2797.
- Duncker, H.-R. 1971. The lung air sac system of birds. A contribution to the functional anatomy of the respiratory apparatus. *Adv. Anat. Embryol. Cell Biol.* 45:1–171.
- Dunning, J. B. Jr. 2008. *CRC handbook of avian body masses*, 2nd ed. CRC Press, Boca Raton, FL.
- Elemans, C. P. 2014. The singer and the song: the neuromechanics of avian sound production. *Curr. Opin. Neurobiol.* 28:172–178.
- Eastman, J. M., L. J. Harmon, and D. C. Tank. 2013. Congruification: support for time scaling large phylogenetic trees. *Methods Ecol. Evol.* 4:688–691.
- Ferguson, M. W. J. 1981. The structure and development of the palate in *Alligator mississippiensis*. *Arch. Oral Biol.* 26:427–443.
- Fletcher, N. H., T. Riede, G. J. L. Beckers, and R. A. Suthers. 2004. Vocal tract filtering and the “coo” of doves. *J. Acoust. Soc. Am.* 116:3750–3756.
- Fletcher, N., T. Riede, and R. A. Suthers. 2006. Model for vocalization by a bird with distensible vocal cavity and open beak. *J. Acoust. Soc. Am.* 119:1005–1011.
- Fitch, W. T. 1999. Acoustic exaggeration of size in birds via tracheal elongation: comparative and theoretical analyses. *J. Zool.* 248:31–48.
- Font, E., and L. C. Rome. 1990. Functional morphology of dewlap extension in the lizard (*Anolis equestris*; Iguanidae). *J. Morphol.* 206:245–258.
- Freeman, A. R., and J. F. Hare. 2015. Infrasonic in mating displays: a peacock’s tale. *Anim. Behav.* 102:241–250.
- Gans, C. and P. F. A. Maderson. 1973. Sound producing mechanisms in recent reptiles: review and comment. *Am. Zool.* 13:1195–1203.

- Garstang, M., D. Larom, R. Raspet, and M. Lindeque. 1995. Atmospheric controls on elephant communication. *J. Exp. Biol.* 198:939–951.
- Gaunt, A. S., S. L. L. Gaunt, H. D. Prange, and J. S. Wasser. 1987. The effects of tracheal coiling on the vocalizations of cranes (Aves: Gruidae). *J. Comp. Physiol. A* 161:43–58.
- Gelman, A., and J. Hill. 2007. *Data analysis using regression and multi-level/hierarchical models*. Cambridge Univ. Press, Cambridge, UK.
- Geyikoglu, F., A. Temelli, and A. Özkartal. 2002. Muscle fiber types of the tunica muscularis externa at the upper part of the sparrow (*Passer domesticus*) esophagus. *Turk. J. Zool.* 26:217–221.
- Gill, F., and D. Donsker (eds). 2015. *IOC world bird list (v 5.4)*. Available at <http://www.worldbirdnames.org/> (accessed December 28, 2015).
- Goodwin, D. 1986. *Crows of the world*. 2nd ed. British Museum of Natural History, UK.
- Goller, F., and R. A. Suthers. 1996. Role of syringeal muscles in gating airflow and sound production in singing brown thrashers. *J. Neurophysiol.* 75:867–876.
- Goller, F., and R. A. Suthers. 1999. Bilaterally symmetrical respiratory activity during lateralized birdsong. *J. Neurobiol.* 41:513–523.
- Goller, F., M. J. Mallinckrodt, and S. D. Torti. 2004. Beak gape dynamics during song in the zebra finch. *J. Neurobiol.* 59:289–303.
- Goller, F., and T. Riede. 2013. Integrative physiology of fundamental frequency control in birds. *J. Physiology* 107:230–242.
- Gridi-Papp, M. 2008. The structure of vocal sounds produced with the mouth open or with the mouth closed in treefrogs. *J. Acoust. Soc. Am.* 123:2895–2902.
- Halkin, S. L., and C. S. Evans 1999a. *Animal Behav Soc Ann Mtg*. Lewisburg, PA: 1999. Form fits function in the low-frequency calls of emus.
- Halkin, S. L., and C. S. Evans 1999b. *Animal Behav Soc Ann Mtg*. Lewisburg, PA: 1999. Between- and within-sex variation in the low-frequency calls of emus.
- Handford, P., and M. A. Mares. 1985. The mating system of ratites and tinamous: an evolutionary perspective. *Biol. J. Linn. Soc.* 25:77–104.
- Hartigan, J. A., and M. A. Wong. 1979. A K-means clustering algorithm. *Appl. Stat.* 28:100–108.
- Hartley, R. S., and R. A. Suthers. 1989. Airflow and pressure during canary song: direct evidence for mini-breaths. *J. Comp. Physiol. A* 165:15–26.
- Hedges, S. B., J. Marin, M. Suleski, M. Paymer, and S. Kumar. 2015. Tree of life reveals clock-like speciation and diversification. *Mol. Biol. Evol.* 32:835–845.
- Hersch, G. L. 1966. *Bird voices and resonant tuning in helium-air mixtures*. Ph.D. thesis, University of California, Berkeley, CA.
- Ho, L. S. T., and C. Ané. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Syst. Biol.* 63:397–408.
- Hopkins-Dubansky, B. 2012. *The functional morphology of the intermandibulo-cervical envelope of the American alligator (Alligator mississippiensis)*. Ph.D. thesis, Louisiana State University, Baton Rouge, LA.
- Ingelfinger, F. J. 1958. Esophageal motility. *Physiol. Rev.* 38:533–584.
- Ives, A. R., and T. Garland. 2010. Phylogenetic logistic regression for binary dependent variables. *Syst. Biol.* 59:9–26.
- Jarvis, E. D. et al. 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* 346:1320–1331.
- Jean, A. 2001. Brain stem control of swallowing: neuronal network and cellular mechanisms. *Physiol. Rev.* 81:929–969.
- Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers 2012. The global diversity of birds in space and time. *Nature* 491:444–448.
- Johnsgard, P. A. 1961. Tracheal anatomy of the Anatidae and its taxonomic significance. *Wildfowl* 12:58–69.
- . 1964. Comparative behavior and relationships of the eiders. *Condor* 66:113–129.
- Katz, P. S. 2012. Neural mechanisms underlying the evolvability of behaviour. *Phil. Trans. R. Soc. B* 366:2086–2099.
- Kilner, R. 1997. Mouth colour is a reliable signal of need in begging canary nestlings. *Proc. Roy. Soc. London B* 264:963–968.
- King, A. S. 1989. Functional anatomy of the syrinx. Pp. 105–192 in A. S. King and J. McLelland, eds. *Form and function in birds*, vol. 4. Academic Press, London, UK.
- Krakauer, A. H., M. Tyrrell, K. Lehmann, N. Losin, F. Goller, and G. L. Patricelli. 2009. Vocal and anatomical evidence for two-voiced sound production in the greater sage-grouse *Centrocercus urophasianus*. *J. Exp. Biol.* 212:3719–3727.
- Lee, M. S. Y., A. Cau, D. Naish, and G. J. Dyke. 2014. Sustained miniaturization and anatomical innovation in the dinosaurian ancestors of birds. *Science* 345:562–565.
- Luschei, E. S., and L. J. Goldberg. 1981. Neural mechanisms of mandibular control: mastication and voluntary biting. In: *Handbook of Physiology*, Baltimore, 1981, Williams & Wilkins.
- Mack, A. L., and J. Jones. 2003. Low-frequency vocalizations by cassowaries (*Casuarius* spp.). *Auk* 120:1062–1068.
- Maddison, W. P. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* 44:539–557.
- Maddison, W. P., and D. R. Maddison. 1992. *Mac-Clade: analysis of phylogeny and character evolution*. Version 3.0. Sinauer, Sunderland, Massachusetts.
- Madsen, V., T. J. S. Balsby, T. Dabelsteen, and J. L. Osorno. 2004. Bimodal signaling of a sexually selected trait: gular pouch drumming in the magnificent frigatebird. *Condor* 106:156–160.
- Maina, J. N. 2005. *The lung-air sac system of birds. Development, structure, and function*. Springer, Berlin, Germany.
- Martin, E. G., and C. Palmer. 2014. Air space proportion in pterosaur limb bones using computed tomography and its implications for previous estimates of pneumaticity. *PLoS ONE* 9:e97159.
- Mason, N. A., and K. J. Burns. 2015. The effect of habitat and body size on the evolution of vocal displays in Thraupidae (tanagers), the largest family of songbirds. *Biol. J. Linn. Soc.* 114:538–551.
- McLelland, J. 1989. Larynx and trachea. Pp. 69–103 in A. S. King and J. McLelland, eds. *Form and function in birds*, vol. 4. Academic Press, London, UK.
- Merton, D. V., R. B. Morris, and I. A. E. Atkinson. 1984. Lek behaviour in a parrot: the kakapo *Strigops habroptilus* of New Zealand. *Ibis* 126:277–283.
- Meyer, G. W., R. M. Austin, C. E. Brady III, and D. O. Castell. 1986. Muscle anatomy of the human esophagus. *J. Clin. Gastroenterol.* 8:131–134.
- Miller, E. H., J. Williams, S. E. Jamieson, H. G. Gilchrist, and M. L. Mallory. 2007. Allometry, bilateral asymmetry and sexual differences in the vocal tract of common eiders *Somateria mollissima* and king eiders *S. spectabilis*. *J. Avian Biol.* 38:224–233.
- Müller, J. 1847. Über die bisher unbekanntenen typischen Verschiedenheiten der Stimmorgane der Passerinen. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin* 1845:321–391 + 6 plates. (English translation: Müller, J. 1878. On certain variations in the vocal organs of the Passeres that have hitherto escaped notice. Oxford at the Clarendon Press, London, England).
- Murton, R. K., and A. J. Isaacson. 1962. The functional basis of some behaviour in the woodpigeon *Columba palumbus*. *Ibis* 104:503–521.

- Murie, J. 1867. *On the tracheal pouch of the emu, Dromeus novaehollandiae*. Proc. Zool. Soc. Lond. 35:405–415.
- Noble, J. C. 1975. Difference in size of emus on two contrasting diets on the riverine plain of New South Wales. *Emu* 75:35–37.
- Nowicki, S. 1987. Vocal tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere. *Nature* 325:53–55.
- Ohms, V. R., P. C. Snelderwaard, C. ten Cate, and G. J. L. Beckers. 2010. Vocal tract articulation in zebra finches. *PLoS ONE* 5:e11923.
- Ohms, V. R., G. J. L. Beckers, C. ten Cate, and R. A. Suthers. 2012. Vocal tract articulation revisited: the case of the monk parakeet. *J. Exp. Biol.* 215:85–92.
- Patapoutian, A., B. J. Wold, and R. A. Wagner. 1995. Evidence for developmentally programmed transdifferentiation in mouse esophageal muscle. *Science* 270:1818–1821.
- Pierko, M. 2010. Structural analysis of upper respiratory tract in *Anas platyrhynchos* (L., 1758) and *Clangula hyemalis* (L., 1758). *Electron. J. Polish Agric. Univ.* 13:22. Available at <http://www.ejpau.media.pl/volume13/issue4/art-22.html>.
- Podos, J., J. A. Southall, and M. R. Rossi-Santos. 2004. Vocal mechanics in Darwin's finches: correlation of beak gape and song frequency. *J. Exp. Biol.* 207:607–619.
- Puglisi, L., M. Pagni, C. Bulgarelli, and N. E. Baldaccini. 2001. The possible functions of call organization in the bittern (*Botaurus stellaris*). *Ital. J. Zool.* 68:315–321.
- Reese, A. M. 1945. The laryngeal region of *Alligator mississippiensis*. *Anat. Rec.* 92:273–277.
- Reichard, D. G., and Welkin, J. F. 2015. On the existence and potential functions of low-amplitude vocalizations in North American birds. *Auk* 132:156–166.
- Revell, L. J. 2011. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3:217–223.
- Riebel, K. 2009. Song and female mate choice in zebra finches: a review. Pp. 197–238 in M. Naguib, V. M. Janik, K. Zuberbühler, and N. S. Clayton, eds. *Vocal communication in birds and mammals. Advances in the study of behavior*, vol. 40. Academic Press, Amsterdam, The Netherlands.
- Riede, T., G. J. L. Beckers, W. Blevins, and R. A. Suthers. 2004. Inflation of the esophagus and vocal tract filtering in ring doves. *J. Exp. Biol.* 207:4025–4036.
- Riede, T., W. Forstmeier, B. Kempnaers, and F. Goller. 2015. The functional morphology of male courtship displays in the pectoral sandpiper (*Calidris melanotos*). *Auk* 132:65–77.
- Riede, T., and F. Goller. 2010. Peripheral mechanisms for vocal production in birds—differences and similarities to human speech and singing. *Brain Lang.* 115:69–80.
- Riede, T., N. Schilling, and F. Goller. 2013. The acoustic effect of vocal tract adjustments in zebra finches. *J. Comp. Physiol. A* 199:57–69.
- Riede, T., R. A. Suthers, N. Fletcher, and W. E. Blevins. 2006. Songbirds tune their vocal tract to the fundamental frequency of their song. *Proc. Nat. Acad. Sci.* 103:5543–5548.
- Riede, T., and R. A. Suthers. 2009. Vocal tract motor patterns and resonance during constant frequency song: the white-throated sparrow. *J. Comp. Physiol. A* 195:183–192.
- Riede, T., I. T. Tokuda, J. B. Munger, and S. L. Thompson. 2008. Mammalian laryngeal air sacs add variability to the vocal tract impedance: physical and computational modeling. *J. Acoust. Soc. Am.* 124:634–647.
- Riede, T., I. T. Tokuda, and C. G. Farmer. 2011. Subglottal pressure and fundamental frequency control in contact calls of juvenile *Alligator mississippiensis*. *J. Exp. Biol.* 214:3082–3095.
- Rudegeair, T. 1975. The gular pouch of the female white ibis. *Auk* 92:168–169.
- Ryan, M. J., and M. A. Guerra. 2014. The mechanism of sound production in túngara frogs and its role in sexual selection and speciation. *Curr. Opin. Neurobiol.* 28:54–59.
- Sacchi, R., P. Galeotti, M. Fasola, and G. Gerzeli. 2004. Larynx morphology and sound production in three species of testudinidae. *J. Morph.* 261:175–183.
- Saino, N., R. M. Ayala, G. Boncoraglio, and R. Martinelli. 2008. Sex difference in mouth coloration and begging calls of barn swallow nestlings. *Anim. Behav.* 75:1375–1382.
- Schmidt, R. S. 1966. Central mechanisms of frog calling. *Behaviour* 26:251–285.
- Seddon, N. 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution* 59:200–215.
- Slabbekoorn, H., S. DeKort, and C. ten Cate. 1999. Comparative analysis of perch-coo vocalizations in *Streptopelia* doves. *Auk* 116:737–748.
- Slabbekoorn, H., and C. ten Cate. 1996. Responses of collared doves to playback of coos. *Behav. Proc.* 38:169–174.
- Smith, S. A., and B. C. O'Meara. 2012. treePL: divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics* 28:2689–2690.
- Speich, S., and D. A. Manuwal. 1974. Gular pouch development and population structure of Cassin's auklet. *Auk* 91:291–306.
- Starnberger, I., D. Preininger, and W. Hödl. 2014. The anuran vocal sac: a tool for multimodal signaling. *Anim. Behav.* 97:281–288.
- Stevens, K. N. 2000. *Acoustic phonetics*. MIT Press, Cambridge, MA.
- Suthers, R. A. 1990. Contributions to birdsong from the left and right sides of the intact syrinx. *Nature* 347:473–477.
- Suthers, R. A., J. R. Rothgerber, and K. K. Jensen. 2015. Lingual articulation in songbirds. *J. Exp. Biol.* 219:491–500.
- Titze, I. R., T. Riede, and P. Popolo. 2008. Nonlinear source-filter interaction in phonation—experimental evidence. *J. Acoust. Soc. Am.* 123:1902–1915.
- Turner, A. H., D. Pol, J. A. Clarke, G. M. Erickson, and M. A. Norell. 2007. A basal dromaeosaurid and size evolution preceding avian flight. *Science* 317:1378–1381.
- Vergne, A. L., M. B. Pritz, and N. Mathevon. 2009. Acoustic communication in crocodylians: from behaviour to brain. *Biol. Rev.* 84:391–411.
- Uriona, T. J., C. G. Farmer, J. Dazely, F. Clayton, and J. Moore. 2005. Structure and function of the esophagus of the American alligator (*Alligator mississippiensis*). *J. Exp. Biol.* 208:3047–3053.
- Wade, J. 1998. Sexual dimorphisms in the brainstem of the green anole lizard. *Brain Behav. Evol.* 52:46–54.
- Webber, T., and R. A. Stefani. 1990. Evidence of vocal learning by a scrub jay. *Auk* 107:202–204.
- Wedel, M. J. 2009. Evidence for bird-like air sacs in saurischian dinosaurs. *J. Exp. Zool. A* 311:611–628.
- Westneat, M. W., J. H. Long, W. Hoese, and S. Nowicki. 1993. Kinematics of birdsong: functional correlation of cranial movements and acoustic features in sparrows. *J. Exp. Biol.* 182:147–171.
- Wetmore, A. 1918. A note on the tracheal air-sac in the ruddy duck. *Condor* 20:19–20.
- Wild, J. M., F. Goller, and R. A. Suthers. 1998. Inspiratory muscle activity during bird song. *J. Neurobiol.* 36:441–453.

Yoshida, M. 2001. A light microscope study of the distribution of muscle in the frog esophagus and stomach. *J. Smooth Muscle Res.* 37:95–104.

Zeigler, H. P., and P. Marler (eds.). 2008. *Neuroscience of birdsong*. Cambridge Univ. Press, Cambridge, UK.

Zweers, G. A., H. C. van Pelt, and A. Beckers. 1981. Morphology and mechanics of the larynx of the pigeon (*Columba livia L.*): a drill-chuck system (Aves). *Zoomorphology* 99:37–69.

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