

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 (Rudegear 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

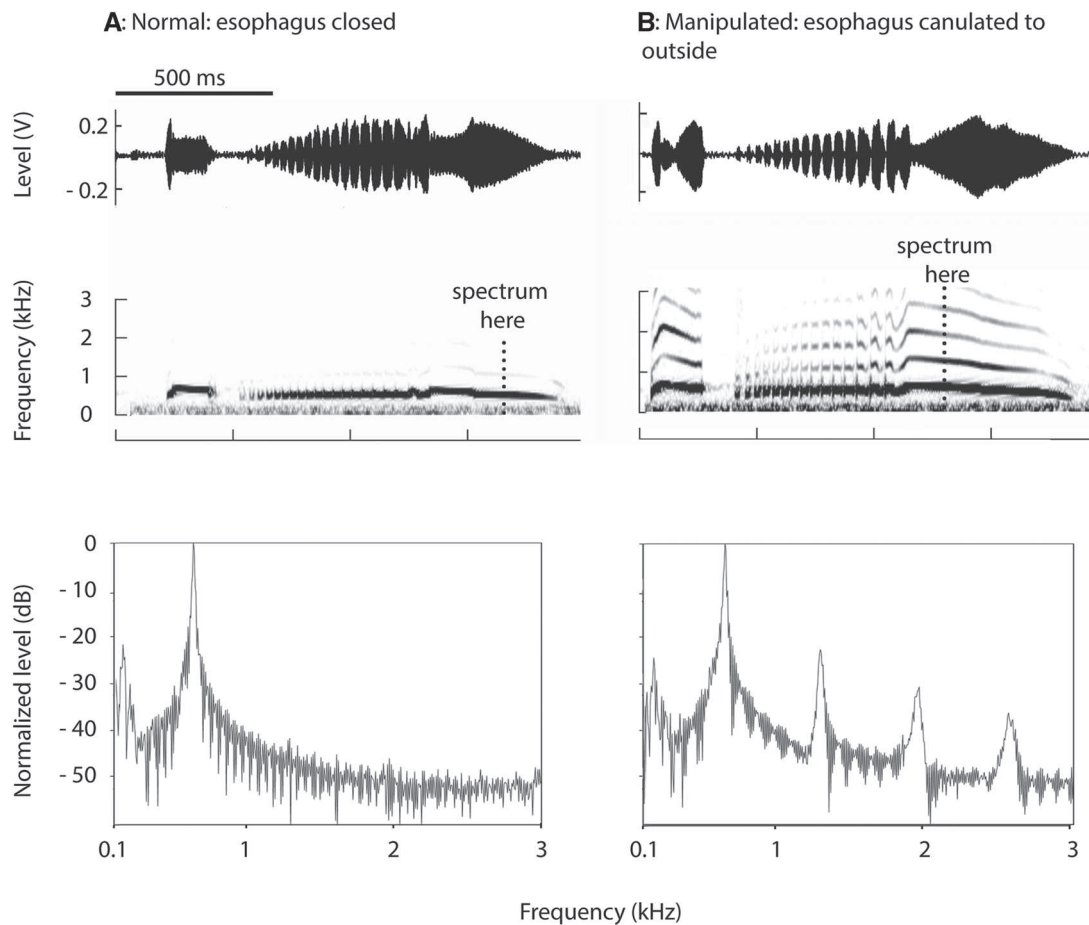


Figure 1. The inflated esophagus of doves and pigeons filters high frequencies of syringeally produced calls during closed-beak vocal behaviors. (A) Normal *coo* call, with esophagus closed to outside. (B) Call produced when the esophagus is open to outside air through a cannula. The calls were uttered 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

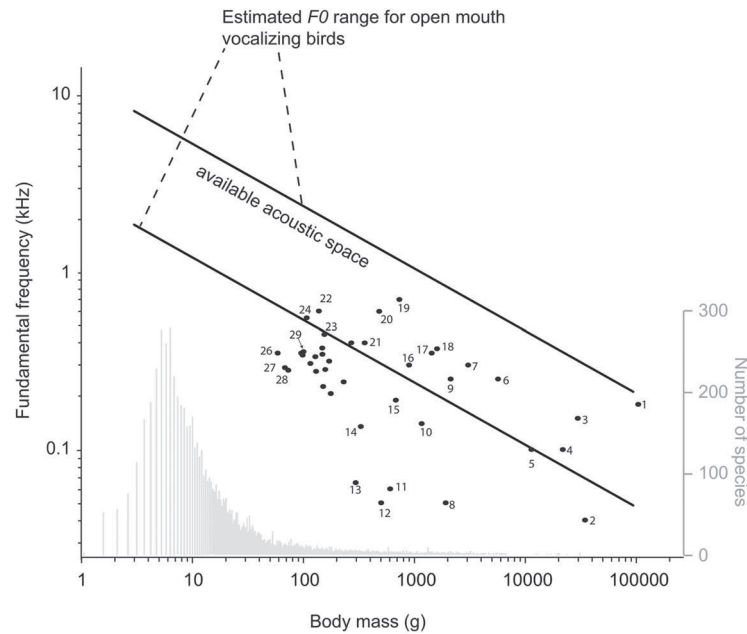


Figure 2. Fundamental frequency (F_0) of vocalizations in birds that vocalize with the mouth closed (closed-mouth vocalization species) is lower than predicted from body size alone. The two black lines indicate the estimated lower and upper boundaries for F_0 range based on body size. The area between the two lines approximates the “available acoustic space” for vocalizing birds, and was estimated based on a simplified string model of the syrinx 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, specktaled 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).

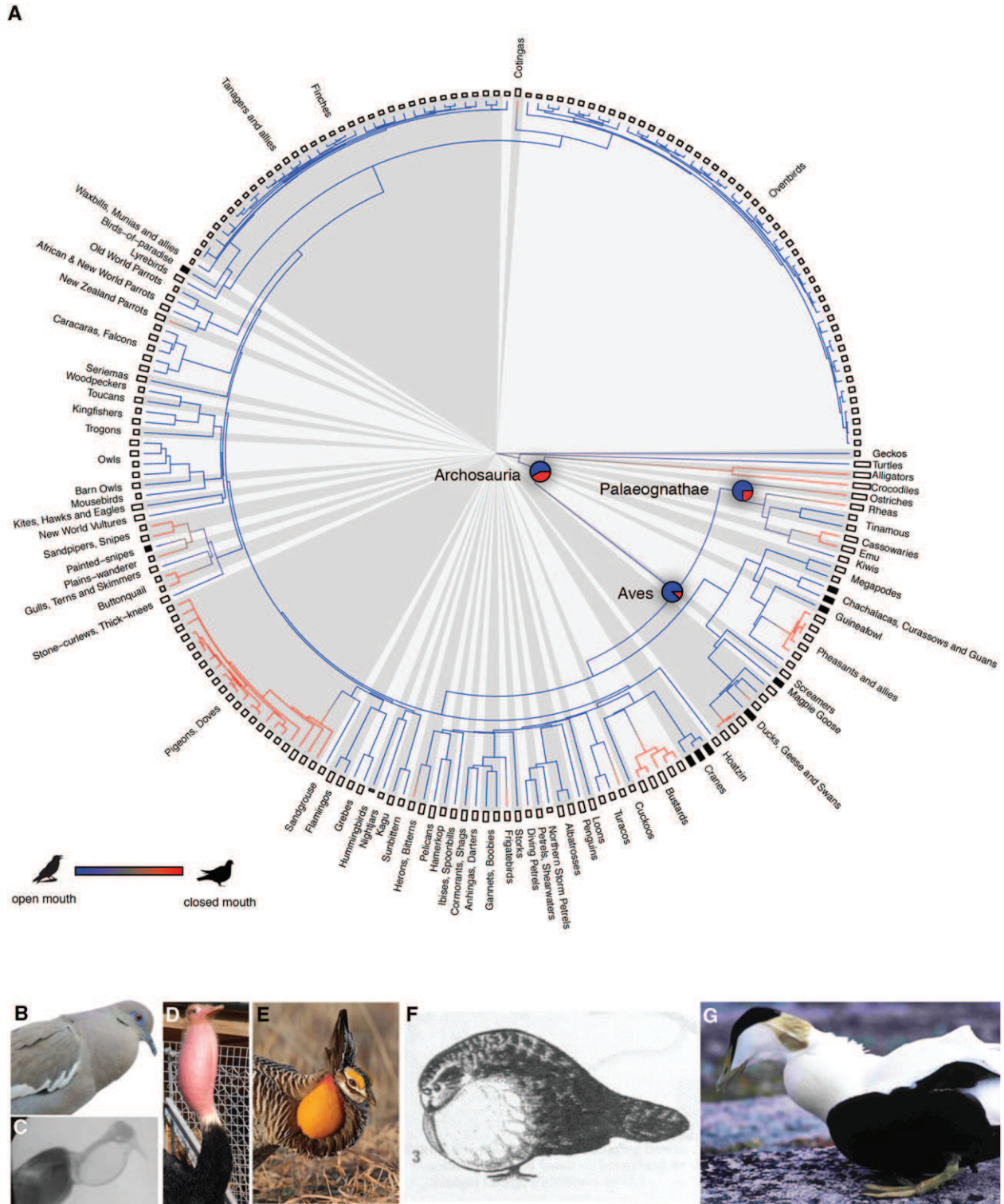


Figure 3. Maximum likelihood ancestral state reconstruction of closed-beak vocal behaviors in birds. (A) Line colors in phylogeny correspond with the probability that the ancestral state was open-mouth (blue) or closed-mouth (red) vocalization. Bars at tips of phylogeny correspond to natural log-transformed body mass, with colors indicating species with nonelongated (white) or elongated (black) tracheae. Phylogeny based on Burleigh et al. (2015), with shaded regions corresponding to bird families indicated. Branch lengths are in units of time (My). The estimated probability of closed-mouth vocalization in the ancestral archosaur is 0.42. Pictures show males of the following species while vocalizing with closed beak and inflating esophagus; (B) ring dove and (C) ring dove x-ray image (image by T. Riede), (D) ostrich, (E) Lesser Prairie-Chicken, (F) kakapo (from Merton et al. 1984), (G) common eider (with permission from Kerrich McKay). Images in B, D, and E are still images from video sources cited in Table S4.

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; Geyikoğlu 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; Luschi 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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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Supplemental Material

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

Tobias Riede¹, Chad Eliason², Edward H. Miller³, Franz Goller⁴, Julia Clarke²

Supplemental Material

Content	Page
Supplementary Methods and Results	1
<i>Taxon sampling and ancestral state reconstruction</i> (Figure S1)	3
<i>Phylogeny choice and ancestral state reconstruction</i> (Figure S2)	5
<i>Body size ancestral state reconstruction and its relationship with vocalization behavior</i> (Table S1)	6
<i>Relationship of closed-mouth vocalization and body mass in birds</i> (Figure S3)	7
<i>Pattern of evolutionary changes in vocal behavior and body mass</i> (Figure S4)	8
<i>Contingent states test</i> (Table S2)	10
Summary of all species investigated in phylogenetic analysis (Table S3)	11
Video and literature sources (Table S4)	18
References	26

Supplementary Methods and Results

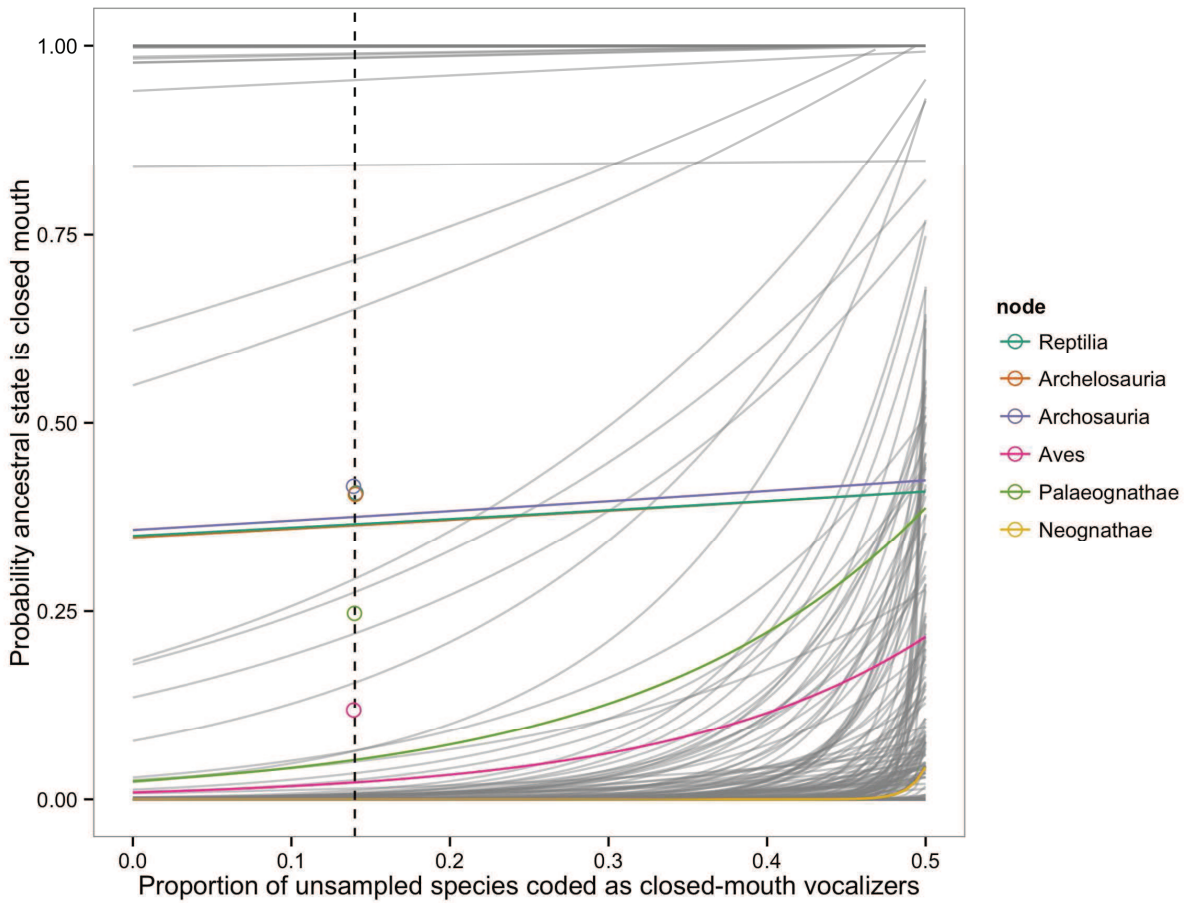
Taxon sampling and ancestral state reconstruction

To assess the impacts of incomplete taxon sampling on our ancestral state reconstruction analyses, we followed Odom et al. (2014). Briefly, we used the 6714-taxon supertree of Burleigh et al. (2015), adding 15 species without genetic data to the root node of the most inclusive clade containing their congeners, along with five outgroup taxa. We then randomly assigned closed-mouth vocalization as a trait in proportions ranging from 0 to 0.5 in increments of 0.05 (the observed proportion of closed-mouth vocalization species in our dataset was 0.15) to avian taxa for which data on vocal behavior were unavailable. Thus, in our most extreme case, 50% of taxa within Aves presently unsampled for vocal behavior were coded as closed-mouth vocalizers. It should be noted that it is not likely that most or even 50% of unsampled Aves (mostly passerines) will be discovered to be closed-mouth vocalizers even though they have not been studied in this context.

Next, we reconstructed ancestral states using these tip values and the estimated rate of character evolution derived from previous model fitting (see above) using the ancRECON function in corHMM (Beaulieu et al. 2013). We repeated this procedure 10 times at each proportion, and compared the mean ancestral state estimates for all nodes to the values estimated with the pruned phylogeny and no missing data. Results are reported in Figure S1. Although the estimated most likely ancestral state for Palaeognathae is more labile with increasing proportions of taxa inferred to be closed-mouth vocalizers than that for Aves and Neognathae, in no case does it become more likely than open-mouth vocalization at any of these nodes.

Figure S1. Sensitivity of ancestral state reconstruction to incomplete taxon sampling.

Horizontal grey lines indicate the probabilities that a given node is estimated to have the state closed-mouth vocalization as a function of the proportion of unsampled species coded as closed-mouth vocalizers. Points are recovered ancestral state optimization of the trait at key nodes, with the observed proportion of closed-mouth vocalizers in our dataset (18%) indicated by a vertical dashed line. Archelosauria (Crawford et al. 2015) refers to the clade described by the most recent common ancestor of Testudines (turtles) plus Archosauria.



Phylogeny choice and ancestral state reconstruction

To assess whether and how phylogenetic uncertainty affected ancestral state reconstructions of vocal behavior, we estimated ancestral states and character-transition rates to/from closed-mouth vocalization across a set of 500 posterior trees from Jetz et al. (2012). Figure S2 shows the effect of phylogeny choice on the inferred probability of closed-mouth vocal behavior at key nodes.

The probability that closed-mouth vocal behavior is ancestral decreases when the phylogeny of Jetz et al. (2012) is used. This difference is attributable to the placement of tinamous as the sister taxon of ratites in Jetz et al. (2012). Current phylogenetic analyses reconstruct ratites as paraphyletic, with ostriches (*Struthio camelus*) as the sister taxon to all other palaeognaths (Mitchell et al. 2014). Given that ostriches are closed-mouth vocalizers (Table S3), this would increase the probability that the palaeognath ancestor was a closed-mouth vocalizer. Both analyses yielded similar transition rates between open- and closed-mouth vocalization (Burleigh: $q = 0.0044$, Jetz: $q = 0.0031$ [0.0029, 0.0034]), as well as a similar number of gains (Jetz: 13-16; Burleigh: 16) and losses of closed-mouth vocalization within Archosauria (Burleigh: 1; Jetz: 1-3).

Figure S2. The effect of phylogeny choice on the ancestral-state reconstruction of vocal behavior (i.e., open- or closed-mouth vocalization). Points show estimated probabilities that the ancestor at the indicated node showed closed-mouth vocal behavior for a given reference phylogeny (open circles; Jetz et al. 2012; **closed** circles, Burleigh et al. 2015). Horizontal lines are 95% confidence intervals calculated across the posterior set of Jetz et al. (2012) trees.

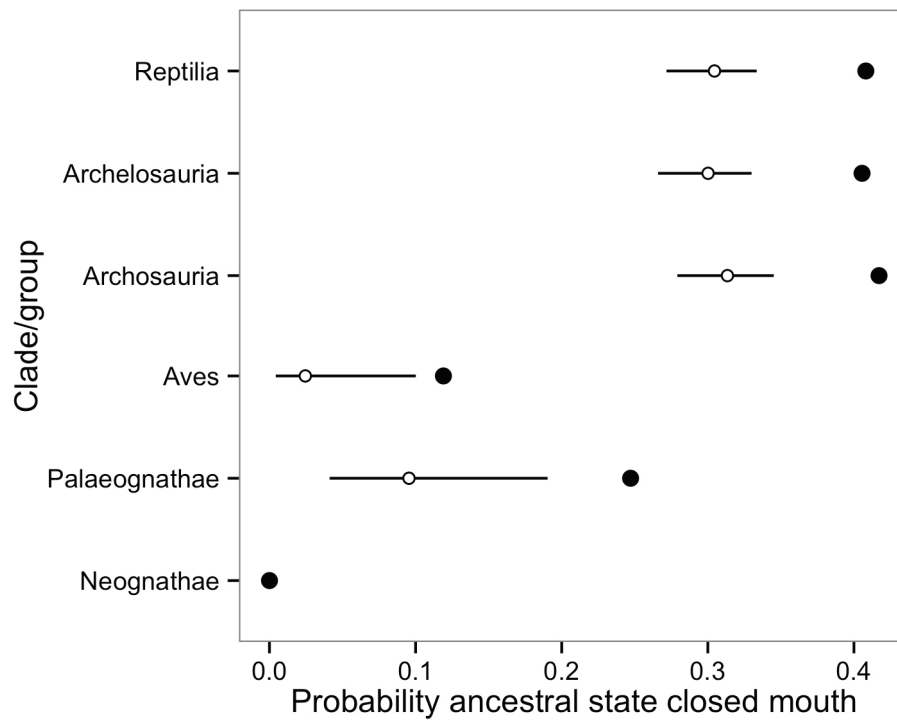


Table S1. Phylogenetic logistic regression results for the relationship of closed-mouth vocalization to body mass. Confidence intervals were calculated based on 2000 bootstrap simulations.

	Estimate	Lower CL	Upper CL	Z	P
Intercept	-0.56	-3.4	0.73	-0.52	0.60
Slope	0.00059	-0.080	0.22	0.0061	1.0
Alpha	0.012	0.0058	0.049		

Figure S3. Relationship of closed-mouth vocalization and body mass in birds. Plot shows vocal behavior (open- or closed-mouth vocalization) versus body mass (n = 208). Lines show results of non-phylogenetic (dashed) and phylogenetic logistic regressions (solid). Shaded region is 95% confidence interval. The relationship of vocal behavior to body mass was not significant after taking phylogeny into account (Table S3). Points were jittered along the y-axis to reduce over-plotting. Silhouettes depict bird species spanning the observed range of body sizes: small (*Emberiza* sparrow), medium (great tinamou, *Tinamus major*) and large (ostrich, *Struthio camelus*). Image credits: L. Shyamal (sparrow), George Edward Lodge (tinamou), and Matt Martyniuk (ostrich). Large species are not more likely to use closed-mouth vocalizations than small species.

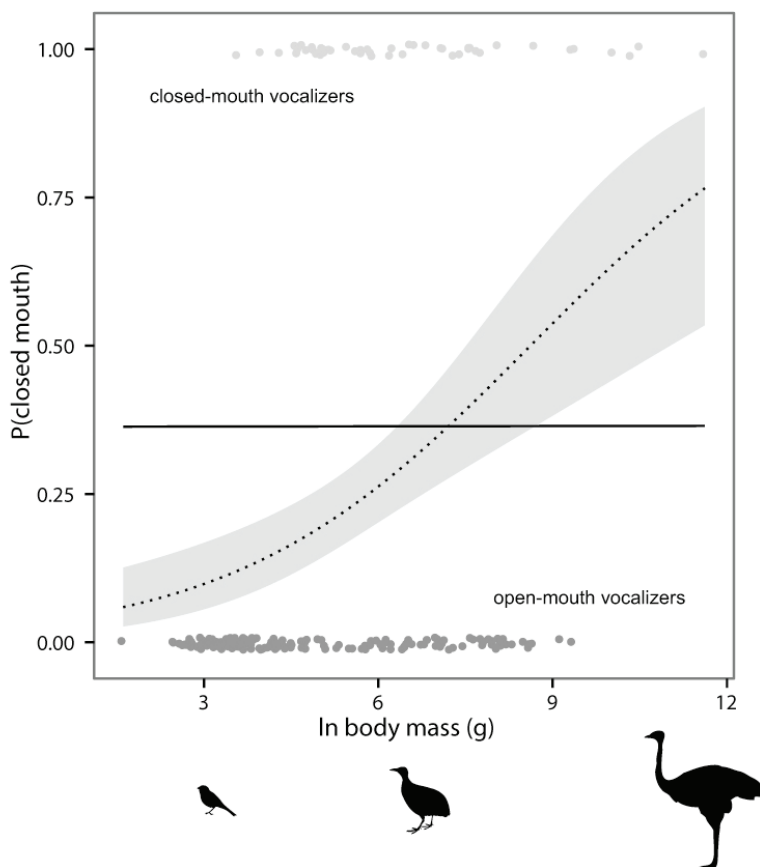
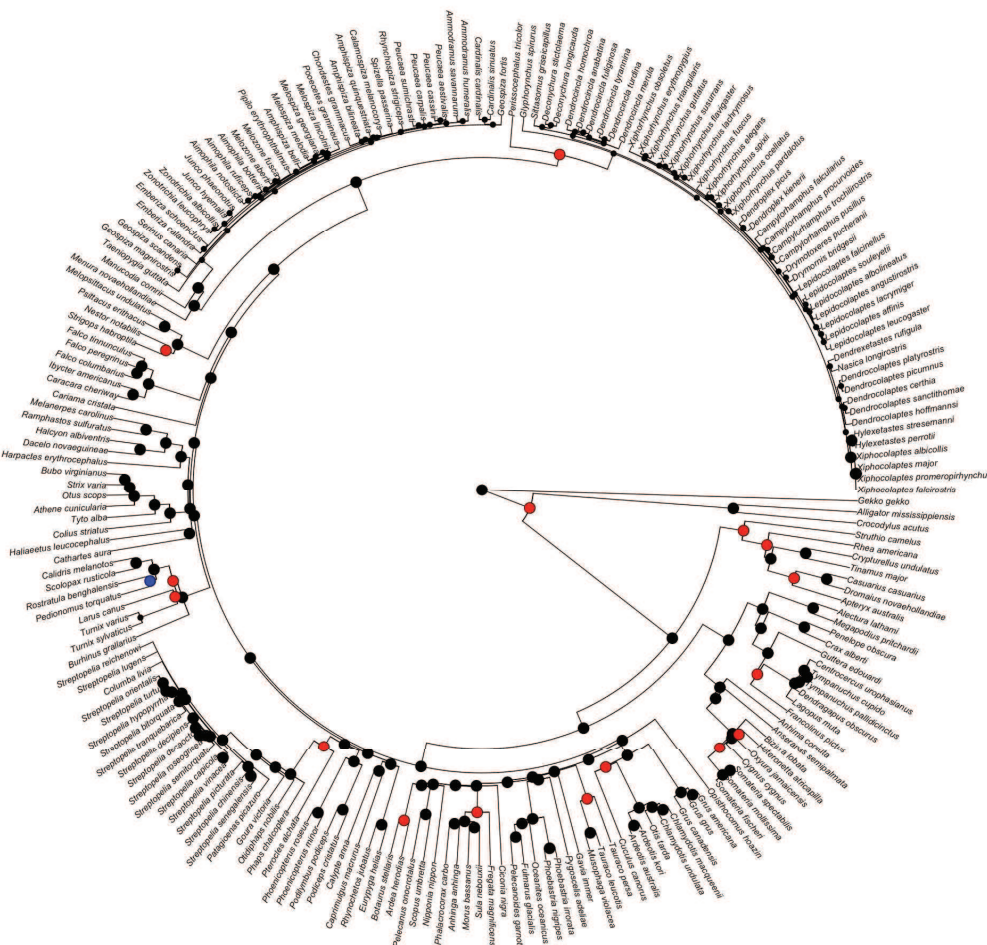


Figure S4. Pattern of evolutionary changes in vocalization behavior and body mass. Node sizes correspond to reconstructed ancestral state of body size (small: < 100 g; large: > 100 g) using the phylogeny of Burleigh et al. (2015) plus outgroups. Node colors indicate where gains (red) and losses (blue) of closed-mouth vocalization occur (ancestral states of vocal behavior are shown in Fig. 3). For example, red color of the passerine ancestral node indicates that a ‘gain’ of closed-mouth vocalization occurred (in the capuchinbird lineage). The ancestral state of passerines was estimated as open-mouth, as indicated in Fig. 3. Ancestral states were reconstructed with maximum likelihood using rayDISC in the coHMM R package. The origin of closed-mouth vocalization was always preceded by an increase in body size.



Contingent states test

Our analysis of the relationship between body size and vocalization behavior was limited to the 211 species with behavioral data (Fig. S3). Thus, to assess the effects of incomplete taxon sampling on our results (specifically, the estimation of ancestral body sizes in birds shown in Fig. S4), we also reconstructed ancestral states using the phylogeny in Burleigh et al. (2015) and a large dataset of body masses (Dunning 2008). We then retained ancestral body size estimates (small or large) that corresponded to nodes in the pruned 211 species phylogeny and tested whether gains of closed-mouth vocalization were more likely to occur in large-bodied lineages using a contingent states test (Sillén-Tullberg 1993). Three groups were estimated as ancestrally small- rather than large-bodied using the expanded body size dataset: Passeriformes, Apodiformes, and Coraciimorphae (*sensu* Jarvis et al. 2014; includes kingfishers, woodpeckers, and trogons). Results of the contingent states test are shown in Table S2. Body sizes reconstructed using the reduced (211 taxa) and full datasets (5576 taxa) both showed a significant relationship between evolutionary gains of closed-mouth vocalization and large body size in birds.

Table S2 Distribution of evolutionary events in vocal behavior along branches

reconstructed as either small- or large-bodied. Contingency table shows number of times open-mouth vocalization was retained (0→0) and closed-mouth vocalization behavior gained (0→1) along a branch in the phylogeny. For the full body size dataset, body size was reconstructed using all available body mass data for birds (Dunning 2008) and a large avian phylogeny (~6700 tips; Burleigh et al. 2015), plus outgroups that was subsequently pruned down to the same tips used in other analyses (Fig. S4). Ancestral states were reconstructed using maximum likelihood using rayDISC in the corHMM R package (Beaulieu et al. 2013). Note: number of origins of closed-mouth vocalization within Archosauria differs from ancestral state reconstruction in Fig. 3 (16 gains) because only branches reconstructed as small or large (and not changing along the branch) were retained for the analysis.

Body size	Vocal behavior		Statistical test result
	0 → 0	0 → 1	
<i>211 taxon dataset</i>			
Small	158	0	$X^2 = 8.61, df = 1, p < 0.001$
Large	225	15	
<i>Full dataset</i>			
Small	171	0	$X^2 = 9.23, df = 1, p < 0.001$
Large	212	14	

Supplemental Table S3: Summary of all species investigated in phylogenetic analysis. Names follow Gill and Donsker (2015). (0: open-mouth vocalization only, OB; 1: closed-mouth vocalization with esophagus inflation, CB; 2: inflatable tracheal diverticulum, TS). Body masses are from Dunning (2008). Fundamental frequency ($F0$) is given only for closed-mouth vocalization species. Values were used from published data where possible (sources listed in table S4) or measured from audio recordings in the sound archive Xeno-Canto.org. Sound analysis was performed with PRAAT (praat.org). Video links and literature citations are provided in Table S4.

	Species	Common name	body mass (g)	OB/EI/TS	F0 closed-mouth (Hz)
2	<i>Tinamus major</i>	Great tinamou	960	0	
3	<i>Crypturellus undulatus</i>	Undulated tinamou	510	0	
4	<i>Apteryx mantelli</i>	North Island brown kiwi	2100	0	
5	<i>Dromaius novaehollandiae</i>	Emu	31500	2	150
6	<i>Casuaris casuaris</i>	Southern cassowary	40000	1	40
7	<i>Rhea americana</i>	Greater rhea	23000	1	100
8	<i>Struthio camelus</i>	Ostrich	111000	1	180
9	<i>Oxyura jamaicensis</i>	Ruddy duck	629	2	60
9a	<i>Somateria spectabilis</i>	King eider	1668	1	370
9b	<i>Somateria fischeri</i>	Spectacled eider	1494	1	350
9c	<i>Somateria mollissima</i>	Common eider	2218	1	250
10	<i>Cygnus cygnus</i>	Whooper swan	9350	0	

11	<i>Anseranas semipalmata</i>	Magpie goose	2766	0	
12	<i>Anhima cornuta</i>	Horned screamer	3150	0	
13	<i>Centrocercus urophasianus</i>	Greater Sage-grouse	3190	1	300
14	<i>Dendragapus obscurus</i>	Dusky grouse	1200	1	86
15	<i>Tympanuchus cupido</i>	Greater prairie chicken	933	1	300
16	<i>Tympanuchus pallidicinctus</i>	Lesser prairie chicken	762	1	700
17	<i>Francolinus pictus</i>	Painted francolin	400	0	
18	<i>Lagopus muta</i>	Rock ptarmigan	521	1	50 (pulsed)
19	<i>Crax alberti</i>	Blue-billed curassow	2500	0	
19a	<i>Penelope obscura</i>	Dusky-legged guan	1770	0	
20	<i>Guttera pucherani edouardi</i>	Crested guineafowl (part)	1149	0	
21	<i>Alectura lathamii</i>	Australian brushturkey	2520	0	
22	<i>Megapodius pritchardii</i>	Tongan megapode	365	0	
23	<i>Phoebastria nigripes</i>	Black-footed albatross	3400	0	
23a	<i>Phoebastria irrorata</i>	Waved albatross	3750	0	
24	<i>Fulmarus glacialis</i>	Northern fulmar	650	0	
25	<i>Oceanites oceanicus</i>	Wilson's storm petrel	32	0	
26	<i>Pelecanoides garnotii</i>	Peruvian diving petrel	202	0	
27	<i>Podiceps cristatus</i>	Great crested grebe	730	0	
28	<i>Podilymbus podiceps</i>	Pied-billed grebe	474	0	

29	<i>Streptopelia turtur</i>	European turtle dove	132	1	334
29a	<i>Spilopelia senegalensis</i>	Laughing dove	101	1	341
29b	<i>Streptopelia tranquebarica</i>	Red turtle dove	103	1	357
29c	<i>Streptopelia vinacea</i>	Vinaceous dove	110	1	552
29d	<i>Streptopelia reichenowi</i>	White-winged collared dove	119	1	306
29e	<i>Streptopelia decipiens</i>	Mourning collared dove	134	1	276
29f	<i>Streptopelia capicola</i>	Ring-necked dove	142	1	602
29g	<i>Streptopelia decaocto</i>	Eurasian collared dove	152	1	374
29h	<i>Streptopelia bitorquata</i>	Island collared dove	153	1	345
29i	<i>Streptopelia lugens</i>	Dusky turtle dove	155	1	227
29j	<i>Streptopelia roseogrisea</i>	African collared dove	155	1	250
29k	<i>Spilopelia chinensis</i>	Spotted dove	159	1	446
29l	<i>Streptopelia hypopyrrha</i>	Adamawa turtle dove	162	1	283
29m	<i>Streptopelia semitorquata</i>	Red-eyed dove	176	1	315
29n	<i>Nesoenas picturatus</i>	Malagasy turtle dove	182	1	207
29o	<i>Streptopelia orientalis</i>	Oriental turtle dove	238	1	241
30	<i>Otidiphaps nobilis</i>	Pheasant pigeon	500	1	600
31	<i>Columba livia</i>	Rock dove	369	1	400
32	<i>Goura victoria</i>	Victoria crown pigeon	2384	1	250
33	<i>Otidiphaps n. nobilis</i>	Pheasant pigeon (part)	500	1	
34	<i>Phaps chalcoptera</i>	Common bronzewing	344	1	
35	<i>Patagioenas picazuro</i>	Picazuro pigeon	279	1	400

36	<i>Pterocles alchata</i>	Pin-tailed sandgrouse	250	0	
37	<i>Tauraco persa</i>	Guinea turaco	306	0	
38	<i>Musophaga violacea</i>	Violet turaco	360	0	
38a	<i>Tauraco leucotis</i>	White-cheeked turaco	265	0	
39	<i>Cuculus canorus</i>	Common cuckoo	117	0	
40	<i>Otis tarda</i>	Great bustard	11975	1	100
41	<i>Chlamydotis macqueenii</i>	Macqueen's bustard	1500	1	
42	<i>Chlamydotis undulata</i>	Houbara bustard	1960	1	50
43	<i>Ardeotis australis</i>	Australian bustard	5970	1	250
44	<i>Ardeotis kori</i>	Kori bustard	11300	1	
45	<i>Grus americana</i>	Whooping crane	5826	0	
46	<i>Grus canadensis</i>	Sandhill crane	4800	0	
46a	<i>Grus grus</i>	Common crane	5500	0	
47	<i>Calypte anna</i>	Anna's hummingbird	4.5	0	
48	<i>Opisthocomus hoazin</i>	Hoatzin	696	0	
49	<i>Calidris melanotos</i>	Pectoral sandpiper	98	1	350
49b	<i>Scolopax rusticola</i>	Eurasian woodcock	306	1	65
49a	<i>Rostratula benghalensis</i>	Greater painted-snipe	121	0	
50	<i>Turnix sylvaticus</i>	Common buttonquail	70	1	350
51	<i>Turnix sylvaticus</i>	Small buttonquail	37	1	290
	<i>lepuranus</i>	(part)			
52	<i>Turnix varius</i>	Painted buttonquail	75	1	280
53	<i>Burhinus grallarius</i>	Bush stone-curlew	672	0	

54	<i>Larus canus</i>	Mew gull	432	0	
55	<i>Pedionomus torquatus</i>	Plains-wanderer	54	1	
56	<i>Eurypyga helias</i>	Sunbittern	210	0	
57	<i>Rhynochetos jubatus</i>	Kagu	860	0	
58	<i>Pygoscelis adeliae</i>	Adelie penguin	5000	0	
59	<i>Botaurus stellaris</i>	Eurasian bittern	1209	1	140
60	<i>Botaurus lentiginosus</i>	American bittern	706	1	190
61	<i>Ardea herodias</i>	Great blue heron	2480	0	
62	<i>Pelecanus onocrotalus</i>	Great white pelican	11450	0	
63	<i>Scopus umbretta</i>	Hamerkop	472	0	
64	<i>Gavia immer</i>	Great northern loon	5400	0	
66	<i>Fregata magnificens</i>	Magnificent frigatebird	1250	1	drumming
67	<i>Morus bassanus</i>	Northern gannet	2932	0	
68	<i>Sula nebouxii</i>	Blue-footed booby	1283	0	
69	<i>Phalacrocorax carbo</i>	Great cormorant	3240	0	
70	<i>Anhinga anhinga</i>	Anhinga	1235	0	
71	<i>Geronticus eremita</i>	Northern bald ibis	1202	0	
72	<i>Ciconia nigra</i>	Black stork	2926	0	
73	<i>Cathartes aura</i>	Turkey vulture	1800	0	
74	<i>Phoenicopterus roseus</i>	Greater flamingo	3000	0	
75	<i>Phoebastria minor</i>	Lesser flamingo	1500	0	
76	<i>Falco tinnunculus</i>	Common kestrel	200	0	

77	<i>Falco peregrinus</i>	Peregrine falcon	894	0	
77a	<i>Falco columbarius</i>	Merlin	163	0	
78	<i>Caracara cheriway</i>	Northern crested caracara	1117	0	
78a	<i>Ibycter americanus</i>	Red-throated caracara	624	0	
79	<i>Melopsittacus undulatus</i>	Budgerigar	30	0	
80	<i>Psittacus erithacus</i>	Grey parrot	350	0	
81	<i>Strigops habroptila</i>	Kakapo	2000	1	50 (pulsed)
82	<i>Nestor notabilis</i>	Kea	956	0	
83	<i>Cariama cristata</i>	Red-legged seriema	1400	0	
84	<i>Strix varia</i>	Barred owl	632	0	
85	<i>Bubo virginianus</i>	Great horned owl	914	0	
86	<i>Athene cunicularia</i>	Burrowing owl	146	0	
87	<i>Tyto alba</i>	Western barn owl	330	0	
88	<i>Otus scops</i>	Eurasian scops owl	85	0	
89	<i>Haliaeetus leucocephalus</i>	Bald eagle	4130	0	
90	<i>Caprimulgus macrurus</i>	Large-tailed nightjar	66	0	
92	<i>Dacelo novaeguineae</i>	Laughing kookaburra	313	0	
93	<i>Halcyon albiventris</i>	Brown-hooded kingfisher	65	0	
94	<i>Melanerpes carolinus</i>	Red-bellied woodpecker	73	0	

95	<i>Ramphastos sulfuratus</i>	Keel-billed toucan	433	0	
96	<i>Harpactes erythrocephalus</i>	Red-headed trogon	80	0	
97	<i>Colius striatus</i>	Speckled mousebird	51	0	
98	<i>Perissocephalus tricolor</i>	Capuchinbird	360	1	140
99	<i>Taeniopygia guttata</i>	Zebra finch	15	0	
100	<i>Menura novaehollandiae</i>	Lyrebird	1100	0	
100a	<i>Manucodia comrii</i>	Curl-crested manucode	448	0	
101	42 species	Fringillidae	15-80	0	
102	64 species	Furnariidae	10-70	0	
Outgroups					
103	<i>Alligator mississippiensis</i>	American alligator	450000	1	
104	<i>Crocodylus acutus</i>	American crocodile	900000	1	
105	<i>Gekko gekko</i>	Tokay gecko	62	0	
106	Multiple species	Testudinidae		0	

Table S4: Video and literature sources for birds vocalizing with an open or closed beak.

	Species	Common name	Video link/reference
2	<i>Tinamus major</i>	Great tinamou	TR, FG personal observation
3	<i>Crypturellus undulatus</i>	Undulated tinamou	https://www.youtube.com/watch?v=1DoGzCHdjOc
4	<i>Apteryx mantelli</i>	North Island brown kiwi	https://www.youtube.com/watch?v=TihMH5Nn-0w
5	<i>Dromaius novaehollandiae</i>	Emu	King and McLelland 1989; Murie 1867 https://www.youtube.com/watch?v=KkHuzdEwnbY
6	<i>Casuarius unappendiculatus</i>	Northern cassowary	http://www.youtube.com/watch?v=YfPIIAEVZuE https://www.youtube.com/watch?v=nuSVLMHUkvQ
7	<i>Rhea americana</i>	Greater rhea	http://neotropical.birds.cornell.edu/portal/species/identification?p_p_spp=55956
8	<i>Struthio camelus</i>	Ostrich	http://www.youtube.com/watch?v=ob1HjQ0UgcY http://www.youtube.com/watch?v=AzVEsLeCdis
9	<i>Oxyura jamaicensis</i>	Ruddy duck	King and McLelland 1989; Murie 1867
9a	<i>Somateria spectabilis</i>	King eider	Johnsgard 1964
9b	<i>Somateria fischeri</i>	Spectacled eider	Johnsgard 1964
9c	<i>Somateria mollissima</i>	Common eider	Johnsgard 1964
9d	<i>Biziura lobata</i>	Musk duck	Johnsgard 1965
9e	<i>Heteronetta atricapilla</i>	Black-headed duck	Johnsgard 1965
10	<i>Cygnus cygnus</i>	Whooper swan	https://www.youtube.com/watch?v=stlA9Tp92bA

11	<i>Anseranas semipalmata</i>	Magpie goose	https://www.youtube.com/watch?v=Y6SmYswf7ak
12	<i>Anhima cornuta</i>	Horned screamer	http://www.youtube.com/watch?v=xXY5LecaoFE http://www.youtube.com/watch?v=1esf6WNdvso
13	<i>Centrocercus urophasianus</i>	Greater Sage-grouse	Clarke et al. 1942, Dantzker et al. 1999 https://www.youtube.com/watch?v=m0M8pZnNlnI
14	<i>Dendragapus obscurus</i>	Dusky grouse	https://www.youtube.com/watch?v=I5qhWJdskw0 https://www.youtube.com/watch?v=dcDBmxSMyTM
15	<i>Tympanuchus cupido</i>	Greater prairie chicken	Schwartz 1945 https://www.youtube.com/watch?v=uEOtNg6SpUY
16	<i>Tympanuchus pallidicinctus</i>	Lesser prairie chicken	https://www.youtube.com/watch?v=CvyjRmHoqfg
17	<i>Francolinus pictus</i>	Painted francolin	https://www.youtube.com/watch?v=j8JWGuf91iY
18	<i>Lagopus muta</i>	Rock ptarmigan	MacDonald 1968
19	<i>Crax alberti</i>	Blue-billed curassow	https://www.youtube.com/watch?v=1x5hZpCfZQ8
19a	<i>Penelope obscura</i>	Dusky-legged guan	https://www.youtube.com/watch?v=XIXcaLrQ6P0
20	<i>Guttera pucherani edouardi</i>	Crested guineafowl (part)	https://www.youtube.com/watch?v=_L9Sj1RCVYQ
21	<i>Alectura lathami</i>	Australian brushturkey	https://www.youtube.com/watch?v=V-BDipgNCU8
22	<i>Megapodius pritchardii</i>	Tongan megapode	Göth et al. 1999
23	<i>Phoebastria nigripes</i>	Black-footed albatross	Sparling 1977
23a	<i>Phoebastria irrorata</i>	Waved albatross	https://www.youtube.com/watch?v=SFwgCh1hh4U

24	<i>Fulmarus glacialis</i>	Northern fulmar	Bretagnolle 1996
25	<i>Oceanites oceanicus</i>	Wilson's storm petrel	Bretagnolle 1996
26	<i>Pelecanoides garnotii</i>	Peruvian diving petrel	Bretagnolle 1996
27	<i>Podiceps cristatus</i>	Great crested grebe	Pers. pbservation
28	<i>Podilymbus podiceps</i>	Pied-billed grebe	https://www.youtube.com/watch?v=Ildb1vY-Q44
29	<i>Streptopelia</i> and <i>Spilopelia spp.</i>	16 species	Slabberkoorn et al. 1999; Riede et al. 2004; https://www.youtube.com/watch?v=SuLMpKx0LF0
30	<i>Otidiphaps nobilis</i>	Pheasant pigeon	http://www.youtube.com/watch?v=dDtpAvIbSpw
31	<i>Columba livia</i>	Rock dove	Pers. observation
32	<i>Goura victoria</i>	Victoria crown pigeon	http://www.youtube.com/watch?v=FML6-w7Eg9w http://www.youtube.com/watch?v=65h3er7BKCY
33	<i>Otidiphaps n. nobilis</i>	Pheasant pigeon (in part)	https://www.youtube.com/watch?v=WdctS6LDffU
34	<i>Phaps chalcoptera</i>	Common bronzewing	https://www.youtube.com/watch?v=wygNi9tXEJc
35	<i>Patagioenas picazuro</i>	Picazuro pigeon	https://www.youtube.com/watch?v=jy49YyPQb_E
36	<i>Pterocles alchata</i>	Pin-tailed sandgrouse	https://www.youtube.com/watch?v=xBO_6UpXS3E
37	<i>Tauraco persa</i>	Guinea turaco	http://www.youtube.com/watch?v=E2VD2WKZ5_A http://www.youtube.com/watch?v=uVi0WjosH_0 http://www.youtube.com/watch?v=6Fb90aTpIwY
38	<i>Musophaga violacea</i>	Violet turaco	https://www.youtube.com/watch?v=W7opw-_AI7E
38a	<i>Tauraco leucotis</i>	White cheeked turaco	https://www.youtube.com/watch?v=uVi0WjosH_0

39	<i>Cuculus canorus</i>	Common cuckoo	http://www.youtube.com/watch?v=q8dEo1nCnAI
40	<i>Otis tarda</i>	Great bustard	Newton 1862; Cullen 1865; Gewalt 1965 http://usa1.framepool.com/de/shot/387557779 http://www.youtube.com/watch?v=BtSCt_27l9Y
41	<i>Chlamydotis macqueenii</i>	Macqueen's bustard	Cornec et al. 2015
42	<i>Chlamydotis undulata</i>	Houbara bustard	Rybak et al. 2014
43	<i>Ardeotis australis</i>	Australian bustard	Garrod 1874 https://www.youtube.com/watch?v=f5YJYmRt3Aw
44	<i>Ardeotis kori</i>	Kori bustard	Murie 1869 https://www.youtube.com/watch?v=wC3ADdhCZag
45	<i>Grus americana</i>	Whooping crane	https://www.youtube.com/watch?v=UM_GeD8w0QI
46	<i>Grus canadensis</i>	Sandhill crane	https://www.youtube.com/watch?v=lbn8yIq7_LM
47	<i>Calypte anna</i>	Anna's hummingbird	https://www.youtube.com/watch?v=Aii7oqwoFdw https://www.youtube.com/watch?v=S3k1G_THKbY
48	<i>Opisthocomus hoazin</i>	Hoatzin	Strahl 1988
49	<i>Calidris melanotos</i>	Pectoral sandpiper	Riede et al. 2015 https://www.youtube.com/watch?v=cnOUHaD1hdo
49b	<i>Scolopax rusticola</i>	Eurasian woodcock	Zedlitz cited by Cramp and Simmons 1983
49a	<i>Rostratula benghalensis</i>	Greater painted - snipe	https://www.youtube.com/watch?v=oWMR14pvPfc
50	<i>Turnix sylvaticus</i>	Small buttonquail	Neunzig 1921
51	<i>Turnix sylvaticus lepuranus</i>	Small buttonquail (part)	Niethammer 1961

52	<i>Turnix varius</i>	Painted buttonquail	http://ibc.lynxeds.com/video/painted-buttonquail-turnix-varia/wild-female-calling
53	<i>Burhinus grallarius</i>	Bush stone-curlew	https://www.youtube.com/watch?v=Hcmh9cDmt7w
54	<i>Larus canus</i>	Mew gull	https://www.youtube.com/watch?v=8eWtsoAIONU
55	<i>Pedionomus torquatus</i>	Plains-wanderer	https://www.youtube.com/watch?v=WB0z3lwlrc8
56	<i>Eurypyga helias</i>	Sunbittern	http://www.youtube.com/watch?v=cpNWCEig9ls http://www.youtube.com/watch?v=ni0hZ3_zQOU https://www.youtube.com/watch?v=XQ4mteuhy_0
57	<i>Rhynochetos jubatus</i>	Kagu	https://www.youtube.com/watch?v=tn5qqOtyRvw
58	<i>Pygoscelis adeliae</i>	Adelie penguin	https://www.youtube.com/watch?v=Qe0JHFE3lfg
59	<i>Botaurus stellaris</i>	Eurasian bittern	Chapin 1922 https://www.youtube.com/watch?v=M3VUS9SihKc
60	<i>Botaurus lentiginosus</i>	American bittern	https://www.youtube.com/watch?v=ky5IYXhraMg
61	<i>Ardea herodias</i>	Great blue heron	https://www.youtube.com/watch?v=CvhKNn_oeno
62	<i>Pelecanus onocrotalus</i>	Great white pelican	Personal observation (TR)
63	<i>Scopus umbretta</i>	Hamerkop	https://www.youtube.com/watch?v=sJpodEIYEHw
64	<i>Gavia immer</i>	Great northern loon	https://www.youtube.com/watch?v=4UrCRcZ8Pas
66	<i>Fregata magnificens</i>	Magnificent frigatebird	Madsen et al. 2004
67	<i>Morus bassanus</i>	Northern gannet	https://www.youtube.com/watch?v=LsfxG_1sIYI
68	<i>Sula nebouxii</i>	Blue-footed booby	https://www.youtube.com/watch?v=d1cl4WsMkco

69	<i>Phalacrocorax carbo</i>	Great cormorant	Pers. observation
70	<i>Anhinga anhinga</i>	Anhinga	https://www.youtube.com/watch?v=9nydmKMdvJw
71	<i>Geronticus eremita</i>	Northern bald ibis	https://www.youtube.com/watch?v=dyhSmfhq4Cs
72	<i>Ciconia nigra</i>	Black stork	https://www.youtube.com/watch?v=76ixj07wFf0
73	<i>Cathartes aura</i>	Turkey vulture	Lynch 2006
74	<i>Phoenicopterus roseus</i>	Greater flamingo	Personal observation (TR)
75	<i>Phoeniconaias minor</i>	Lesser flamingo	https://www.youtube.com/watch?v=YGwhioGkf5A
76	<i>Falco tinnunculus</i>	Common kestrel	https://www.youtube.com/watch?v=MZrcJKICELQ
77	<i>Falco peregrinus</i>	Peregrine falcon	https://www.youtube.com/watch?v=rVD8EnowIFo
77a	<i>Falco columbarius</i>	Merlin	https://www.youtube.com/watch?v=rVD8EnowIFo
78	<i>Caracara cheriway</i>	Northern crested caracara	https://www.youtube.com/watch?v=z-r36GtFAzY
78a	<i>Ibycter americanus</i>	Red-throated caracara	https://www.youtube.com/watch?v=rAhfTUOKAb8
79	<i>Melopsittacus undulatus</i>	Budgerigar	https://www.youtube.com/watch?v=WVrZ7P4QfcE
80	<i>Psittacus erithacus</i>	Grey parrot	https://www.youtube.com/watch?v=uDjVYbYxs68
81	<i>Strigops habroptila</i>	Kakapo	Merton et al. 1984; https://www.youtube.com/watch?v=XWkFh12KBwo http://ibc.lynxeds.com/video/kakapo-strigops-habroptilus/male-under-bush-preparing-starting-boom-daytime-note-initial-inhal
82	<i>Nestor notabilis</i>	Kea	https://www.youtube.com/watch?v=KZyxBswxVis
83	<i>Cariama cristata</i>	Red-legged seriema	https://www.youtube.com/watch?v=ZmXnxRzYXsQ

84	<i>Strix varia</i>	Barred owl	http://www.youtube.com/watch?v=fppKGJD3Y6c http://www.youtube.com/watch?v=KYTkZ8PZ3EU
85	<i>Bubo virginianus</i>	Great horned owl	http://www.youtube.com/watch?v=p4CRqJJW6S8 https://www.youtube.com/watch?v=N0jVgldCwAk https://www.youtube.com/watch?v=AwEi6TMrOWc
86	<i>Athene cunicularia</i>	Burrowing owl	http://www.youtube.com/watch?v=Ls-vgejqz_8
87	<i>Tyto alba</i>	Western barn owl	https://www.youtube.com/watch?v=JDmRmRb2OpE https://www.youtube.com/watch?v=6sAAkU1H7_w
88	<i>Otus scops</i>	Eurasian scops owl	http://www.youtube.com/watch?v=wkGP2OP7wvc
89	<i>Haliaeetus leucocephalus</i>	Bald eagle	https://www.youtube.com/watch?v=PQ2uMauyBow
90	<i>Caprimulgus macrurus</i>	Large-tailed nightjar	https://www.youtube.com/watch?v=-urA3oVemKU
92	<i>Dacelo novaeguineae</i>	Laughing kookaburra	https://www.youtube.com/watch?v=Fc_-icFHwQo
93	<i>Halcyon albiventris</i>	Brown hooded kingfisher	https://www.youtube.com/watch?v=kQ4WI1K2698
94	<i>Melanerpes carolinus</i>	Red-bellied woodpecker	https://www.youtube.com/watch?v=W-Amtw1okjI
95	<i>Ramphastos sulfuratus</i>	Keel-billed toucan	https://www.youtube.com/watch?v=9LX0aVFvy8s
96	<i>Harpactes erythrocephalus</i>	Red-headed trogon	https://www.youtube.com/watch?v=rLI1kerS22A
97	<i>Colius striatus</i>	Speckled mousebird	https://www.youtube.com/watch?v=ArNx2yrJOrQ
98	<i>Perissocephalus tricolor</i>	Capuchinbird	https://www.youtube.com/watch?v=OJgfcOd1R7E&index=7&list=ELaYy3a60ZYJo (after 28:00)

99	<i>Taeniopygia guttata</i>	Zebra finch	https://www.youtube.com/watch?v=TaC6D1cW1Hs
100	<i>Menura novaehollandiae</i>	Lyre bird	https://www.youtube.com/watch?v=VjE0Kdfos4Y
100	<i>Manucodia comrii</i> <i>a</i>	Curl-crested manucode	https://www.youtube.com/watch?v=ah2c2bz4JiQ
101	42 species	Fringillidae	Podos 1997
102	64 species	Furnariidae	Derryberry et al. 2012
Outgroups			
103	<i>Alligator mississippiensis</i>	American alligator	Uriona et al. 2005; Britton 2001
104	<i>Crocodylus acutus</i>	American crocodile	Britton 2001
105	<i>Gekko gekko</i>	Tokay gecko	Tang et al. 2009; Boehme et al. 1984; Rittenhouse and Russell 1998
106	Multiple species	Testudinidae	Galeotti et al. 2004

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