

S26-5 Vocal sacs and their role in avian acoustic display

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Abstract Much progress has been made in understanding the fundamentals of the avian voice in general and the workings of the syrinx in particular. As well, there is growing understanding that the rest of the avian vocal tract plays an important accessory role in sound production. Here we examine the role that one such secondary structure, the avian vocal sac, may play in shaping the avian voice, addressing its function in chamber resonance, membrane resonance, acoustic coupling, directionality, and percussion. Special attention is given to the greater sage grouse, *Centrocercus urophasianus*, with its paired vocal sacs and unique strut display.

Key words Vocal sac, Sound production, Acoustic display, Greater sage grouse

1 Introduction

Birds produce most of their sounds with their syrinx; and physiologists have spent decades determining how this uniquely avian voice-box works. Having only recently solved the long-standing riddle of how vibrations are produced in the syrinx, the field has now turned to the role of ancillary structures that modify, radiate, and spatially configure those vibrations. It is already clear that these secondary adaptations are even more diverse than the structures creating the initial vibrations.

It has long been realized that the upper vocal tracts of both mammals and birds can act as resonance filters, increasing the tonal quality of song (Greenewalt, 1968; Nowicki, 1987); in humans, this filtering is an essential precondition for speech. Recent work on mammals has shown that vocal tract resonances can also feed back on the non-linear dynamics of the vibrating glottis, and alter the kinds of vibration patterns produced (Mergell and Herzel, 1997; Riede et al., 2000). Birds also modify their vocal tract geometries, and thereby are likely to produce similar effects during vocalization. The best example of this to date comes from studies of changes in beak posture (Westneat et al., 1993), which demonstrated a tight association between beak movements and vocalization. Moreover, differences in vocal tract morphology among species can create species specific differences in sound production. Differences in beak morphology, in particular, have been shown to be important in the diversification of sound signals (Podos, 2001). Hence, in recent years, it has become increasingly apparent that the secondary structures associated with sound production and radiation in birds may have quite profound evolutionary and behavioral significance.

2 Secondary acoustic structures in birds

Given the newly recognized importance of upper vocal tract structure, it is useful to compare the relevant accoutrements that are present in various avian groups. Examples include the tracheae of cranes and swans that form multiple loops within the breast bone, and the upper trachea of ducks that is enlarged to form a chamber (Dorst, 1974). These significantly lengthen or enlarge the path between the syrinx and the outside world. Many such vocal modifications have been described but few have yet had their function rigorously examined. Almost without exception, these structures are presumed to function as “resonators”; but no tests have been done to justify this conclusion. One such trait, one that has evolved many times in birds yet has received no attention as a general phenomenon, is the vocal sac. While all birds have air sacs as part of their respiratory system, and many birds puff up these sacs, their esophagus, and/or their gular region to some extent when vocalizing, only a subset have exaggerated and externally visible sacs. It is this latter group that is the focus in this review.

3 Types of avian vocal sacs

Most avian vocal sacs are bare with few or no feathers. Such bald sacs are found in at least five avian families, including the North American grouse (Tetraonidae) and the Neotropical cotingas (Contingidae) which have perhaps the most striking examples of bare vocal sacs found in birds. In grouse and cotingas, the vocal sacs are only inflated to their largest extent in acoustic display. The vocal sacs are brightly colored in most of these species, and therefore probably involved in concurrent visual signaling. The pantropical frigatebirds (Fregatidae), and two storks, the Old World marabou (*Leptoptilos crumeniferus*) and New World jabiru (*Jabiru mycteria*), also inflate their necks and phonate but not always at the same time. In these species, the

air sac is often held fully inflated for lengthy periods in a strictly visual display and is only used occasionally in sound production. The African pink-backed pelican (*Pelecanus rufescens*) has been reported to make a loud “blowing sound” when it inflates its gular pouch (Serle, 1943), but it is unclear from the description just how vocal the birds are.

Three other groups have vocal sacs that are equally impressive but not devoid of feathers. Perhaps the most striking is the kakapo (*Strigops habroptilus*), an endangered flightless parrot from New Zealand that seems to inflate its whole body when booming. Many medium to large bustards (Otididae) inflate sacs which are often covered in elaborate feathering; and some but not all inflating bustard species vocalize while inflated. Buttonquails (Turnicidae), which inflate as well, are unique insofar as they are the only group in which females, not males, have the vocal sac.

4 Vocal sac functions

What role do vocal sacs play in sound production in birds? Here we examine the various functions that any vocal tract accoutrement might fulfill, and assess their relevance to vocal sacs.

4.1 Chamber resonance

Sets of natural resonant frequencies result from the size and shape of the vocal tract. Introduced vibrations that match the resonant peaks of the vocal tract will experience a relative gain while others will be selectively filtered out. The addition of any air filled space can, in principle, alter the resonant spectrum of the vocal tract and change the character of the voice. This is thought to be the explanation associated with opening and closing the beak (Westneat et al., 1993). Manipulations of beak gape lead to a mismatch between this filter and syringeal output, and the result is less tonal sound (Hoese et al., 2000).

Does the addition of a “balloon” change the resonant properties of the chamber? Certainly the size and shape of the airway are changed with inflation of such a sack, and this in turn should result in a change in the resonant peaks. However, there is some doubt whether a flexibly walled sac can act as an efficient chamber resonator because the transfer of sound across the membrane is so easy that independent vibrations might not be supported (Watkins et al., 1970). When a frog, for example, is made to vocalize in a helium atmosphere in an assay for this kind of resonance, there is no evidence that it plays a significant role (Capranica and Moffat, 1983; Rand and Dudley, 1993).

That the vocal sac of a frog does not amplify or filter its laryngeally-produced sound through selective chamber resonance does not necessarily mean that all air sacs are incapable of such sound modification. If the flexibility of the walls of the anuran vocal sac make it unsuitable for chamber resonance, then perhaps other air sacs consist of materials more suited to the task. Alternatively, the air sacs

of frogs may just be too small to effectively alter the frequency composition of the relatively low frequency sounds that they produce (Ryan, 1988). If so, other animals that use air sacs may have a more appropriate match between frequency output and the size of their inflated air sacs. Many birds call at higher fundamental frequencies than frogs, which would also tend to make chamber resonance a more viable function for their air sacs. Therefore, it is inappropriate to rule out chamber resonance as air sac contribution without appropriate experimentation.

4.2 Selective radiation and coupling

In most tetrapods, internally produced sound is transmitted to the surrounding medium through the nose or mouth. This seemingly simple process is complicated by the impedance mismatch of the apertural air way and the environment. Depending on the shape of the aperture, much of the sound may actually be reflected back into the vocal tract. One way that animals can avoid such problems in transference is to pass the sound through a membrane which has an intermediate impedance value (Bradbury and Vehrencamp, 1998). An inflated air sac has a more favorable impedance match with surrounding air, and therefore is able to transfer sound energy to the environment more efficiently.

This type of trans-membrane sound transfer is frequency dependent since the membrane itself has resonant frequencies. The precise nature of this frequency dependence is determined by the size, shape, and micro-anatomical makeup of the membrane tissue. It is likely that selection has acted to bring the natural resonant frequencies of membranes that couple sounds to the environment into line with important components of species-specific vocalizations.

To understand how relevant this may be for avian vocal sacs we can again learn from research done on the better-studied anuran vocal sac. Frogs call with mouth and nares closed so that all sound must pass across some biological membrane for transmission. Purgue (1997) showed that various anurans have membrane transfer functions with peaks that are aligned with key components of species-specific vocalizations. Thus, the anuran vocal sac is an important selective resonator; but it is the transfer function of the membrane that matters, not that of the chamber. This helps to explain how such small animals can make such low frequency sounds so loudly. It also suggests that selective radiation and coupling might be an important feature of air sacs in many birds, specifically those that, like the greater sage grouse (*Centrocercus urophasianus*) and the kakapo, vocalize at very low frequencies.

4.3 Rapid modulation of resonance

Westneat et al. (1993) showed that rapid movement of the beak during vocalization can have profound effects on the signal emitted. Rapid changes in sac volume or shape might also cause fluctuations in resonance which create qualitatively novel sounds. Such an effect is likely to be found in animals that use their sacs in a dynamic fashion such as sage grouse or the bare-necked umbrellabird

(*Cephalopterus glabricollis*). Through rapid body movements and muscle contractions, these birds modify the shape of their vocal sacs wildly during display, creating rapid changes in the shape of the sac which might alter chamber resonant profiles. This also modulates tension on the membrane which affects its resonance profile. The bare-necked umbrellabird has a fleshy projection attached to the middle-bottom of its air sac (Crandall, 1945) that might serve to amplify both types of modulation.

5.4 Directionality

Air sacs which are used to couple sound to the environment have the potential to modify more than just the frequency composition of those sounds. This mode of radiation also alters the shape of the sound field significantly. An animal that relies on expired air to carry the pressure waves to the environment will have an acoustic field shaped very much like that of a horn. The intensity of the waves will be much greater in line with the opening, and have frequency-dependent lobes of lower intensity to the sides and rear. A single air sac, however, might act much more like an acoustic monopole where pressure waves are of nearly equal intensity in all directions. This is generally what has been found in anurans with a single vocal sac (Gerhardt, 1975). It is less clear what pattern would be radiated from paired sacs.

We examined the directionality of a two sac system in our work on the greater sage grouse (Dantzker et al., 1999). As noted above, adult male sage grouse in breeding condition develop a pair of bare vocal sacs on their breasts. These sacs inflate and deflate many times during each two-second strut display. The display consists of noisy wing sounds followed by several low frequency notes ("coos"), a loud broadband pop, a frequency-modulated high frequency note, and a final pop. Males repeat this same display over and over for hours when lekking. We found that the lower frequency and broadband components of the strut display radiate in a monopole or unidirectional pattern, while the higher frequency components radiate in a variable dipole pattern (Dantzker et al., 1999). This suggests that paired vocal sacs may be used to create spatially variable interference patterns. At least for the greater sage grouse, this produces sounds that are broadcast more laterally than frontally, and are thus unlike any animal sounds previously measured.

5.5 Percussion

In some cases, air sacs may serve not only in the modification of syringeally produced sounds, but also in the production of novel vibrations. The mode of such production is most likely percussion of the inflated air sac. The bare-necked umbrellabird and the sage grouse appear to offer two very different examples of air sac percussion. In one, the male umbrellabird shakes its body from side to side, and the fleshy projection on its vocal sac slaps rhythmically back and forth against the inflated sac to produce a rapid drumming sound (Crandall, 1945). In the sage grouse there are no projections to bang against the inflated air sacs. Instead, the paired air sacs are slapped against each other, possibly producing the loud

"pop" components of the display. These seem to be clear examples of percussion but it is important to bear in mind that the sound produced by percussion may not be the primary reason for the behavior. Rather, the behavior might serve more to start rapid movement of the air sac membrane to lead to the dynamic modulation of resonant and/or radiation patterns described above.

5 Conclusion

Evolutionary biologists see convergence as a signpost for adaptation. The vocal sac appears to be an excellent example of such convergent evolution given that it has evolved independently at least eight times in birds. However, the complexity and diversity of the ways that vocal sacs are used, and the different physical processes that seem to be invoked in different species, suggest that considerably more research on different vocal sac systems will be needed to determine whether this, and other secondary acoustic structures in birds, follow common rules.

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