Observations on sound production in the Anatidae

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It has been known for a long time that, among non-passerine birds, the Anatidae are remarkable for the diversity of specializations in the trachea and syrinx, associated with sound production. It has also been recognised that these variations have taxonomic significance (Heinroth 1911; Johnsgard 1961), but virtually no attempts have been made to correlate the complex tracheal structures with the sounds produced. Yet the group offers many fascinating problems such as the adaptive significance of the looping of the trachea, either outside the body cavity as in the Magpie Goose *Anseranas semipalmata*, or inside the sternum as in the northern swans *Cygnus cygnus* and *C. columbianus*. Additionally, males of many species of ducks, particularly pochards (Aythyini) and sea ducks (Mergini), exhibit irregular enlargements of the tracheal tube. The majority of anatine species also show marked sexual dimorphism in the structure of the syrinx. Asymetrically enlarged bullae are typical in adult males, while females retain the relatively simple condition similar to that found in geese and swans. This paper is a first and perhaps naive attempt to understand the functional significance of such complex variations in waterfowl vocalizations.

General structural and acoustical aspects of sound production

One of the earliest attempts thoroughly to describe the structure of the avian syrinx and relate it to vocalizations was that of Myers (1917), whose description of the domestic fowl's *Gallus gallus* syrinx remains a classic. Rüppell (1933) agreed with Myers that sound produced in the syrinx by vibrating the tympaniform membranes is strongly influenced by the tracheal tube. Myers found that shortening the effective length of the trachea by severing it in the neck region served to raise the pitch of calls from 375 to about 500 cycles per second. As Sutherland and McChesney (1965) have pointed out, this result suggested that the length of the trachea can influence the rate of vibration of the tympaniform membranes, as in a wind instrument. Thorpe (1959) believed that the principle might be applied to many 'primitive' (non-songbird) avian species. Yet, Greenewalt (1968) has recently come to the surprising conclusion (p. 183) that the 'trachea plays no acoustical rôle in avian vocalization', a view that is hardly understandable considering the aforementioned studies.

Harris *et al.* (1968) analysed sound production by means of sonagrams when air was forced through syrinxes of dead roosters. They varied tension on isolated and intact syrinxes, varied the lengths of attached tracheal tubes, and examined the effects of the beak and glottis. They concluded that the fundamental frequency of sound generated by the tympaniform membranes is determined exclusively by the degree of syrinx tension. However, the associated structures (bronchi, trachea, beak and oral cavity) operate as a resonating tube and an associated expansible chamber, tending to tune the vocalizations to a basic resonant frequency. In chickens and similar birds with a uniformly narrow trachea, this resonant frequency is primarily determined by the length of the tracheal tube. The formula used by Harris *et al.* clearly indicates that they visualised this resonating system as being acoustically equivalent to a closed pipe, a reed-pipe instrument. Thus, they calculated that the amplitudes of the fundamental frequency and successive harmonics could be explained on the basis of the tracheal tube and bronchi acting as a single resonating tube.

In contrast, Sutherland and McChesney (1965) used similar sonagraphic techniques to analyse the calls made by living Snow Geese *Anser caerulescens* and Ross's Geese *Anser rossii*. They also calculated resonant frequencies based on the measured (but not indicated) lengths of the tracheal tubes, and on the assumption that the trachea may act either as an open-pipe (trumpet) or closed-pipe (reed instrument) resonating chamber. A tracheal tube acting like a closed pipe would generate a resonant frequency only half as great as an open pipe of the same length, and thus would have correspondingly lower-frequency harmonics. Comparison of the sonagrams with calculated resonant frequencies caused these authors to conclude that the tracheal tube operates in the manner of an open-pipe instrument. The Snow Goose had a lower

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membrane fundamental frequency although the total tympaniform membrane areas and membrane thicknesses of the two species appeared to be approximately the same. The authors therefore concluded that the width of the tympaniform membrane may be more important than either its length or total area in determining its vibration rate.

Both these studies confirmed the basic idea that two different processes are in volved. First, the tympaniform membranes vibrate at a frequency partially regulated by their size or area, but which can be increased by increasing membrane tension. Assuming that the rate of vibration increases in proportion to the square root of tension, a theoretical ninefold increase in tension resulted in a threefold increase in frequency of sounds (Harris *et al.* 1968). Secondly, the tracheal tube and associated respiratory and pharyngeal structures provide a resonating chamber having a basic resonant frequency that is primarily determined by the length of the tracheal tube. The longer the tube, the lower the trachea's resonant frequency, and the greater the number of harmonics that will be generated in the audible range. Since low-frequency sounds have the greatest carrying power, a species that must communicate over great distances clearly needs the longest possible resonating tube. This would provide a possible explanation for the evolution of elongated tracheal tubes in the Magpie Goose and northern swans, as well as in various cranes and cracids.

Greenewalt (1968: 161) doubts this and instead attributes the loud voices of swans and cranes to their ample reserve of available air. As noted above, he questioned the ability of the trachea to modulate their calls, in spite of the marked differences in relative harmonic amplitudes that he reported. Instead he attributed these variations to unexplained mechanical constraints imposed on the tympanic membranes. However, Amadon (1970) noted that species of Cracidae having long tracheae usually have 'booming' voices with great carrying power. He also noted the relatively large size of their syrinxes and associated tympaniform membranes (also found in the northern swans). This would permit a low membrane vibration, and a consequent low fundamental frequency of vocalizations.

Greenewalt suggested (p. 183) that a critical test of tracheal modulation in birds would be to determine whether, in a helium-oxygen atmosphere, the theoretical increase in tracheal resonance frequencies caused an increase in the pitch of the vocalization. Such studies had already been performed by Hersch (1966), who found that at least in the case of the Mallard *Anas platyrhynchos*, the only duck tested, a change in vocal pitch *did* occur. The current evidence thus strongly favours a rôle of tracheal modulation, at least in species possessing fairly long tracheae.

Being controlled by independent factors, there is no *a priori* reason to believe that the fundamental (source-generated) frequency of vibration of the tympaniform membranes should necessarily coincide with the resonant (carrier-generated) frequency of the tracheal tube or any one of its harmonic multiples. Rather, it may be imagined that these two systems come into phase only at certain common harmonic frequencies which would thus be relatively amplified. The harmonics of the fundamental frequency that are not in phase with the resonant frequency harmonics would tend to be dampened out. Such differential amplitude development of 'frequency zones' may clearly be seen in some of the sonagrams accompanying this paper, particularly those of the true ducks. In contrast, some species' calls exhibit relatively uniform development of harmonics from the lowest to the highest frequencies covered by the sonagraph. This is suggestive of a distinct 'tuning' effect, of the trachea on the source-generated fundamental frequency. Not surprisingly, this is especially clear in the northern swans, since the very long trachea produces an extremely low resonant frequency, whose many harmonics are much more likely to be nearly 'matched' with harmonics of the fundamental frequency than are the relatively few and high-pitched resonant frequencies produced by a very short trachea. Thus, the calls of pygmy geese (*Nettapus*) are high-pitched, virtually lacking in harmonics (see Frith 1967: 270), and have a considerable resemblance to the nearly pure-toned calls of whistling ducks (*Dendrocygna*).

Greenewalt (1968: 164) pointed out that for each bird species a frequency threshold for pure whistles apparently exists, above which no audible harmonics are generated and below which one or more harmonics develop. As the fundamental frequencies fall, such harmonic monics becoming progressively dominant over the fundamental ones, higher harmonics becoming progressively dominant as the fundamental frequency falls. This was so up to at least the ninth harmonic and apparently up to the fifteenth in some Trumpeter Swan *Cygnus c. buccinator* calls (p. 160). However, Greenewalt attributed these differential harmonic amplitudes to a transition from a rippling to a more pulse-like membrane vibration, rather than to modulating effects of the trachea.

More recently Wurdinger (1970) has provided an important analysis of the comparative vocalisations of four goose species and their anatomical correlates. She concluded that the necessary variations in tension of the tympanic membranes are regulated by the interclavicular air sac rather than the tracheal muscles. This air sac pressure is also directly correlated with the call's fundamental frequency and amplitude. Differences between species' fundamental frequencies correlate negatively with the area of the tympanic membranes, and the differences in amplitudes correlate negatively with tracheal diameters. Further, the tracheal width may also influence the relative development of harmonics, wider tracheal tubes being associated with the reduction of higher harmonics.

Since the tracheal and syringeal anatomy of the Anatidae varies between the major taxonomic groupings, a short review of the acoustical characteristics of the calls made by species representing the various tribes is now presented. Unless otherwise indicated, the accompanying sonagrams were made with a Kay Audiospectrograph Model 6061B, with frequency ranges of 80 to 8000 cycles per second, wide-band filter, and HS setting. The sequence of discussion follows my earlier (1961) paper on tracheal anatomy, but the tribes Cairinini and Oxyurini are excluded from consideration owing to lack of adequate comparative material. Estimates of fundamental frequencies were determined by two methods. For those species having fairly high fundamental frequencies and thus few harmonics, the frequencies were measured directly from the sonagram baseline, using a calibrated scale. In cases where the fundamental frequencies were relatively low and exhibited strong harmonic development, the frequencies were estimated by determining the frequency range covered by several harmonics and dividing by the number of harmonics (Fouquette 1960). The dominant frequency represents the fundamental frequency or harmonic having the maximum amplitude, as indicated by the relative darkness of the sonagram or by taking a 'section' of the call in its mid-point. Harmonics were numbered by considering the fundamental frequency as zero and the first overtone above it as harmonic number one (whereas Fouquette (1969) numbers the fundamental as the first harmonic).

In the calls of some species, the fundamental frequencies may be obscured by pulsed or trilled characteristics of the sounds. Where the pulse rate of the call is considerably under 100 per second, the human ear detects the pulse rate rather than the audible sound frequencies (McAlister 1959), and the trill or pulse rate can be counted by the number of vertical energy pulses on the sonagram per unit of time. It is not yet clear whether these vertical pulse rates represent actual fundamental frequencies of less than 100 Hz., or whether the pulse rates are independently generated, as in some anuran species (McAlister 1959). The glottis might provide a possible start-stop control of pulsed sounds that would be independent of tracheal resonating effects (Thorpe 1959).

Few data on the actual length of the trachea and associated structures *in situ* are available. Comparisons between dried and fresh specimens in ducks and quails indicated that dried tracheae shorten by between 20 to 50%, making museum specimens quite useless. Audubon (1840-1844) gave some lengths of fresh tracheae when 'moderately' extended, but these are not really precise enough for our purposes. Detailed dissection of a wide range of species is a future requirement to check the estimates of effective tracheal length derived below from acoustical properties.

SUBFAMILY ANSERANATINAE

Tribe Anseranatini (Magpie Goose)

The vocalizations of the monotypic Australian Magpie Goose are of special interest because of the extraordinary length of the adult male's trachea which may reach 150 cm. (Johnsgard 1961), whereas it is considerably shorter in females. This maximum length would allow a remarkably low minimum resonant frequency (about 115 Hz. in an open-pipe system), and the potential for a very large number of resonating harmonic frequencies. Contrary to my earlier (1961) observations, Frith (1967) reported that male Magpie Geese have higher pitched voices than do females, and the sonagrams that he published would support this view.

To resolve this problem, I recorded the

vocalizations of the breeding Magpie Geese at the Wildfowl Trust in May 1971. The adult male was the bird I studied and reported on in 1961, and by 1971 was at least 20 years old, while the two females were six years old. Magpie Goose calls recorded by D. S. McChesney at the Wildfowl Trust involved the same male but two different females. Several individual calls sonagrammed from these recordings indicate that the male calls exhibit fundamental frequency ranging from about 270 to 300 Hz, and have a large number of harmonics that diminish in a relatively progressive fashion, disappearing at about 6,000 Hz. These typically fall slightly in pitch near the end of the call, but in the case of alarm calls, uttered as the bird tosses his bill upwards, the pitch rises slightly during the call. The females' calls exhibit considerable variation in pitch, and it was not possible to determine whether these reflect individual or possible functional or intensity variations. A low volume grunting note uttered in situations of mild disturbance has a fundamental frequency of about 200 Hz and is strongest in harmonics at about 1,000 Hz. Another female call, uttered during apparent excitement, has a considerably higher pitch, with a fundamental frequency of about 520 Hz, and fairly uniform development of harmonics that gradually diminish at higher frequencies. It would thus appear that male Magpie Goose vocalizations, although not consistently lower than those of females, do seem more uniform in pitch, suggesting a distinct 'tuning effect' of the extremely long tracheal tube. Female calls vary considerably in pitch, and may be higher or lower than those of males. Measurements of the tracheal tube lengths for adult females are not available, but those of males could effectively resonate calls with fundamental frequencies as low as 115 Hz.

SUBFAMILY ANSERINAE

Tribe Dendrocygnini (Whistling Ducks)

The whistling ducks have a somewhat surprising sexual dimorphism of the syrinx, with males possessing an oval-shaped tracheal bulla and the females a relatively simpler structure. So far, sonagrams of adult calls from only one species of *Dendrocygna* have been published, by Frith (1967) for the Eyton's Whistling Duck *D. eytoni.* I have prepared sonagrams from three additional species of *Dendrocygna* and of *Thalassornis,* a probable near relative of the whistling ducks (Johnsgard 1967).

The calls of the Fulvous Whistling Duck *D. bicolor* are the most typically anserine, in that they exhibit the least varied overall frequency range and a relatively large number of harmonic frequencies are amplified (Figure 1a). The typical double-note *'wa-kew'* begins with a short (1/20 sec.) rising and falling note ranging in maximum amplitude from about 2,720 to 4,000 Hz. This is immediately followed by a longer (¼ sec.) note that also rises and falls in pitch and with maximum amplitude between 2,400 and 3,600 Hz. The fundamental frequency of the mid-point of this second note appears to be at about 900 Hz., and the nearly uniform development of harmonics suggests that this is near the resonating frequency of the tracheal tube, which thus might be expected to be about 19 cm. long.

The calls of the White-faced *D. viduata* and Red-billed *D. autumnalis* Whistling Ducks differ considerably from those of *bicolor*, both in their more complex temporal and frequency patterning and in their greatly reduced harmonic content (Figures 1b and 1c). Both species have flight calls that consist of three or more major rising and falling syllables and with only one well developed harmonic above the fundamental frequencies and under 8,000 Hz. In *viduata* the frequencies vary from about 2,000 to 3,850 Hz., with the greatest amplitude around 3,500 Hz. The actual fundamental frequency, however, appears to be under 1,000 Hz., with the greatest amplitude thus being apparently generated in the fifth harmonic, and again between 4,500 and 8,000 Hz., particularly around 7,200 Hz. A tracheal tube 24 cm. long would generate a resonating frequency of 717 Hz. with the fifth and tenth harmonics falling at 3,583 and 7,166 Hz., which would nicely account for the observed amplitude increases in these zones.

The flight calls of *autumnalis* have surprising similarities to those of *viduata*, although even more drawn out, and the preliminary rising note is better developed. Again, only two major harmonics are well developed below 8,000 Hz., both of which appear to be multiples of some lower fundamental frequency that is but weakly developed. Some sonagrams clearly indicate that there are four sound zones below the first major zone of sound energy, and four more between the first and the second. The zones of maximum sound production in these two patterns are between 2,880 and 3,760 Hz., and between 6,800 and 7,200 Hz. Again, a tracheal tube of 25 cm. would provide fifth and tenth resonating frequencies of 3,440 and 6,880 Hz.

The White-backed Duck *Thalassornis leuconotus* is most unusual (Figure 1d). It not only differs from the stiff-tailed ducks so far studied, but also shows the rapid and sharp frequency fluctuations characteristic of *Dendrocygna*, as well as a markedly differential amplification of certain harmonics. The calls usually begin fairly low in pitch, suddenly 'break' to a high note with a single dominant harmonic of about 4,500 to 6,000 Hz., that abruptly terminates. The pitch then drops back down to the original strong amplication of several lower harmonics. These lower harmonics are fairly uniformly generated at frequency multiples of about 1,250 Hz., suggesting a resonating tracheal tube length of about 14 cm. Well-developed harmonics in the middle, high-pitched phrase segment are virtually lacking. This suggests that the source-

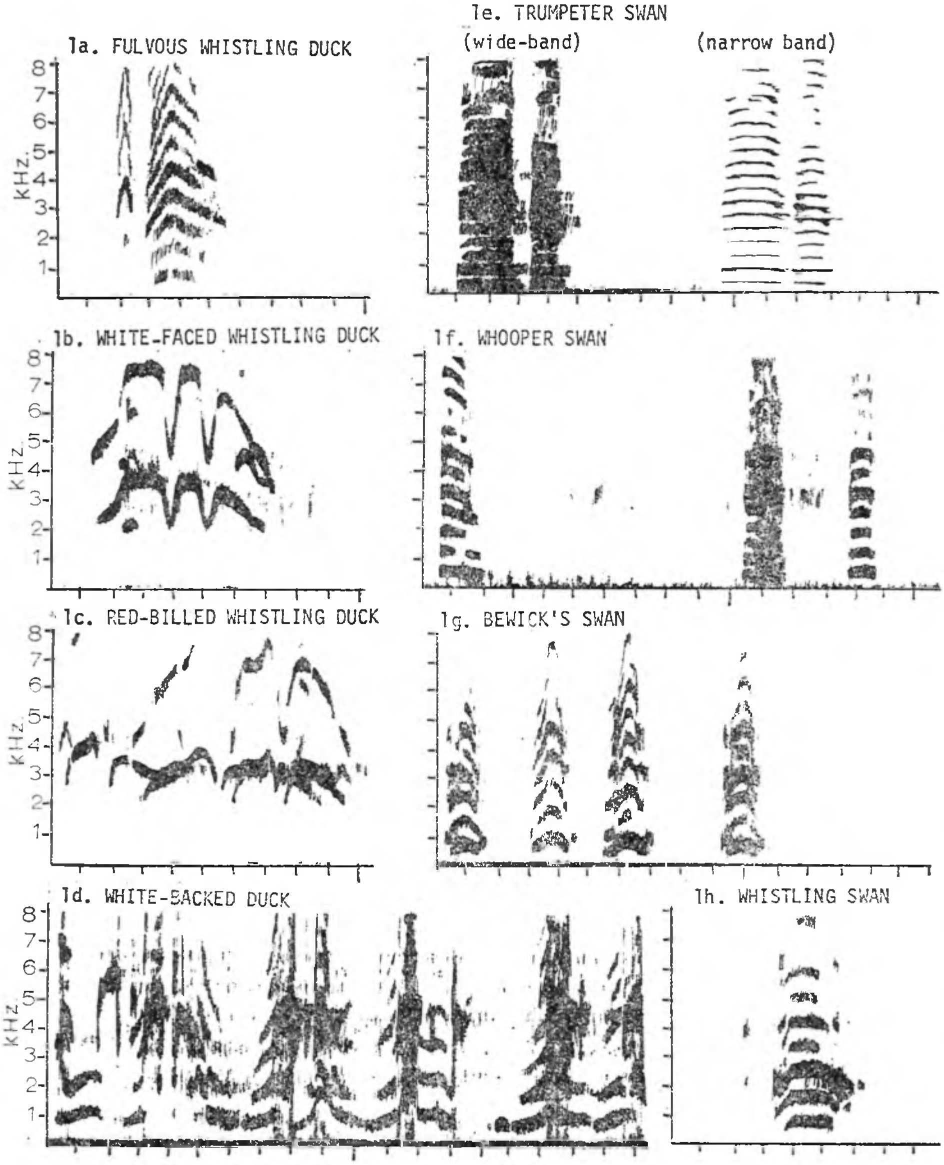


Figure 1. Sonagrams of representative whistling ducks and swans.

generated (tympaniform membrane) fundamental frequency is out of phase with most of the resonating frequencies, while under maximum tension under the syringeal membranes, and finally drops back to the fundamental frequency at which the call started.

Tribe Anserini (Swans and True Geese)

The typical swans *Cygnus* include the arctic-breeders *C. cygnus* and *C. columbianus*, which possess strong voices and tracheal that convolute within the sternum, and three relatively weak-voiced and more temperate-breeding swan species, the Mute *C. olor*, Black *C. atratus* and Black-necked *C. melanocoryphus*. There is also the monotypic Coscoroba Swan *Coscoroba coscoroba*, which has a syringeal structure similar to that of the Mute Swan, but with strong calls of complex harmonic development like those of geese and the northern swans.

Sonagrams (Figures 1e, 1h) are available for all four northern swans, which in sequence from the largest to smallest are the Trumpeter *C. cygnus buccinator*, Whooper *C. cygnus cygnus*, Whistling *C. columbianus columbianus* and Bewick's *C. columbianus bewickii*. When these are compared, it is evident that the larger birds have calls exhibiting less frequency fluctuation than the smaller ones, suggesting that a long tracheal tube may indeed tend to 'tune' the call by placing constraints on the fundamental frequency. Additionally, the fundamental frequencies and thus the number of developed harmonics are correlated with relative body size; in the 80 to 8,000 Hz. range the usual number of harmonics evident were as follows: Trumpeter 17-19 Whooper 12, Whistling and Bewick's 9-10.

Greenwalt (1968) calculated fundamental frequencies for two Trumpeter Swans at 475 and 485 Hz., and two Whistling Swans at 815 and 833 Hz. For the calls shown here, the approximate fundamental frequency in the middle of each call, based on average distances between harmonics, is 461 for the Trumpeter, 666 for the Whooper, 750 for the Whistling, and 800 for the Bewick's Swan. These increasingly higher fundamental frequencies would be expected with the smaller syringeal sizes and shorter tracheal tubes, and could be generated by tracheal tubes of the following lengths and their multiples: 37.3, 26.8, 22.9 and 21.5 cm. Actual measured fresh tracheal lengths of Whistling and Trumpeter Swans have not been published to my knowledge. A fresh adult Whistling Swan trachea examined by Mrs. D. Jean Tate (*in litt.*) measured 117.1 cm. (intrasternal length of 35.1 cm.), with bronchi of 4.1 and 3.0 cm.

The snorting threat uttered by male Mute Swans is curiously pulsed (ca. 55/sec.) (Figure 2b) and, apart from its initial phrasing, develops few harmonics. However, the fundamental frequency of the first phrase appears to be about 720 Hz., which would develop with a tracheal tube length of some multiple of 23 cm., perhaps 69 cm.

By contrast, the Black-necked Swan has a more musical call (Figure 2a) with a fundamental frequency ranging from about 900 to 1,600 Hz. This relatively high figure correlates well with the small size of the adult and its relatively small syrinx. The maximum amplitude of the call occurs at about 960 Hz., which would be in phase with a tracheal tube of 18 cm. or some multiple, perhaps 54 cm.

Sound analyses of the Canada Goose *Branta canadensis* have been made by Greenewalt (1968) and of two species of *Anser* by Sutherland and McChesney (1965). The Canada Goose provides an ideal subject for the influence of tracheal length, since sub-species range in adult size from nearly 9 kg. to under 2 kg. A representative sonagram of a moderately large *B. c. canadensis* race is shown in Figure 2c. This illustrates well that the prolonged, fairly uniform-pitch calls of these birds are quite low: Greenewalt reported fundamental frequencies of 131 and 383 Hz. In Figure 2c, the fundamental frequency is at approximately 510 Hz., and the great amplitudes occur, judging from cross-section study, in the second, fourth, and ninth harmonics, or at intervals of 1,150 Hz. This would correspond to a tracheal length of some multiple of 15 cm. Würdinger (1970) indicated that two Canada Geese that she examined had tracheal lengths of 42.6 and 46.3 cm., as measured in freshly dead specimens.

The relatively small Ne-ne *Branta sandvicensis* has a call with an average fundamental frequency about 670 Hz. (Figure 2d), and consequently a large number of harmonics. These harmonics are amplified especially in the frequencies between 2,000 and 4,000 Hz., primarily at about 2,500 and 3,800 Hz. Again, these frequencies would be resonated well with a tracheal tube length some multiple of 14 cm.

The curious Cereopsis *Cereopsis novaehollandiae*, which might be either anserine or tadornine in its affinities, has a voice (Figure 2e) that is astonishingly similar to that of the Mute Swan's snort.

It has the same rattling trill characteristics of about 40 pulses per second, and a very wide frequency range with few harmonics.

SUBFAMILY ANATINAE

Tribe Tadornini (Shelducks and Sheldgeese)

In this subfamily well-defined sexual dimorphism in tracheal anatomy and adult calls first appears. The calls of the females tend to retain the highly developed harmonic content and the relatively minor frequency variations typical of geese and swans, whereas the males sometimes produce nearly pure whistled sounds having considerable frequency variation. An example of a typical female call is the inciting of the Ruddy Shelduck *Tadorna ferruginea* shown in Figure 2g. Apart from its broken cadence characteristics, it is remarkably like that of the Canada Goose shown in Figure 2c, with a low fundamental frequency that is under 500 Hz., and with differential amplification of the harmonics, particularly in the frequency zones of about 1,000, 2,500 and between 4,000 and 5,000 Hz. This ampli-

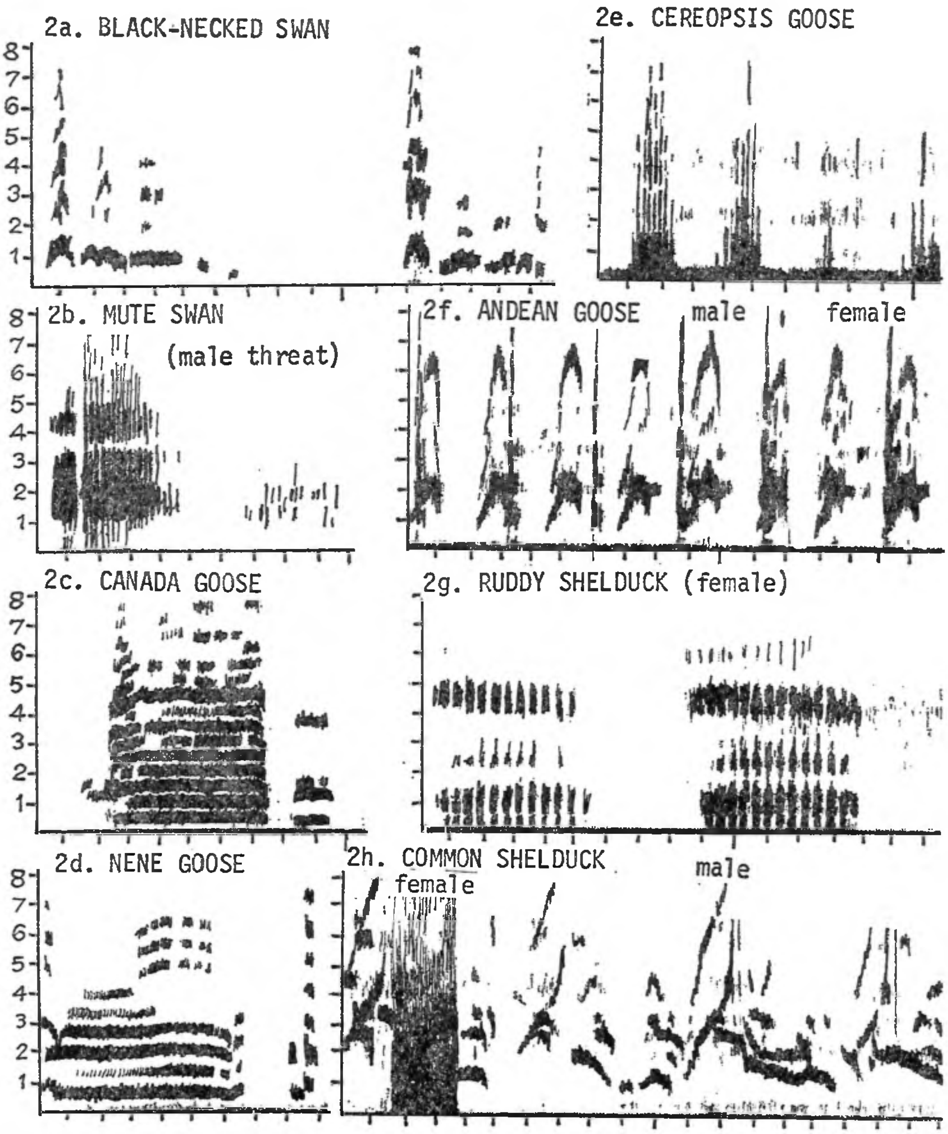


Figure 2. Sonagrams of representative swans, geese and shelducks.

cation could be readily accounted for by a tracheal tube some multiple of 13 cm. in length.

The very low-pitched call of the female Andean Goose *Chloephaga melanoptera* (Figure 2f) has less developed harmonics but several tones of harmonic amplification are evident, as in the male's chuckling notes. In his more sibilant series of *'wi wi'* notes the fundamental frequency fluctuation (from about 1,000 to 2,500 Hz.) becomes more evident and the harmonic bands in the zones around 3,400 and 4,600 Hz. are relatively less amplified, with major amplification instead at 2,170, 3,400 Hz., and again at 4,600 Hz., but not around 4,000 Hz. (Figure 2f). Whether these differences in resonant frequencies are enough to account for the observed damping of sound between 3,400 and 4,600 Hz. is difficult to judge.

Sexual dimorphism in vocalizations is even more pronounced in the Common Shelduck *Tadorna tadorna.* The female calls vary considerably in duration and rate of repetition (up to about seven per second in the case of rapidly repeated cackling notes), and in all cases have a fundamental frequency too low to measure on the sonagrams, but with poor development of resonant harmonics (Figure 2h). In contrast, the whistling notes of the male are fairly pure, mostly in the range of 1,000 to 3,000 Hz., initially rising sharply in pitch, then dropping back more gradually. In the 'casarca' group the males possess a rudimentary tracheal bulla, and the two sexes exhibit only very limited sexual dimorphism, as shown by Frith's (1967) sonagrams for the Australian Shelduck *Tadorna tadornoides.* This would certainly support the view (Johnsgard 1961) that a well developed tracheal bulla is probably responsible for the ability of males of the larger Anatinae to produce pure whistled notes.

Tribe Anatini (Dabbling Ducks)

The number of species of *Anas* and of related genera is far too great to show representative sonagrams from all of them. Frith (1967) has already published sonagrams for the Grey Teal *Anas gibberifrons,* Chestnut Teal *A. castanea,* Australian Black Duck *A. superciliosa* and the aberrant Pink-eared Duck *Malacorhynchus membranaceus.*

Two common calls of adult female Mallard *Anas platyrhynchos* are the inciting call and the decrescendo call (Figure 3a). Besides differing markedly in cadence characteristics, the inciting calls appear to have a lower fundamental frequency that is completely out of phase with the resonating frequencies of the tracheal tube, producing vertical energy bands on the sonagrams, with little if any harmonic structuring. In contrast, the decrescendo call is a series of repetitive notes having nearly the same fundamental frequency but of diminishing amplitude, all with well developed harmonic structure. The fundamental frequency of the call shown is at about 585 Hz., and maximum amplication occurs between 1,500 and 2,500 Hz. Greenewalt (1958) reported a fundamental frequency of 179 Hz. for a female Mallard call, with maximum amplification in the harmonic centering at 1,428 Hz.

The alarm notes of *Anas* females appear to be similar to the decrescendo calls in their acoustic characteristics, but are more uniform in cadence and amplitude (Figures 3b, 3c). The *'raeb'* call of the male is drawn out (0.3 sec.) in a manner similar to the female's alarm notes, and otherwise appears quite similar to them on the sonagrams. As in the female, maximum amplitude occurs around 2,000 Hz.

Whistled notes of the male Mallard are not available for sonagraphic inspection, but the courtship calls of male Gadwall *Anas strepera* interestingly alternate between typical *'raeb'* sounds and whistled notes (Figure 3d). The very low-pitched fundamental frequency of the *'raeb'* notes (estimated at about 105 Hz. from the vertical striations on the sonagrams) is somewhat amplified in the zone around 2,500 Hz., whereas the whistled notes centre on a frequency zone of about 3,300 Hz., with a weak harmonic at 6,600 Hz. It is unlikely that tension changes on the syringeal muscles alone could account for this dramatic shift in frequency, and it instead seems possible that the shift reflects a change from a tympaniform-membrane-generated sound to a bulla-generated sound, on the aeolian whistle principle (Johnsgard 1961). Similarly, the 'cricket' whistle of male European Green-winged Teal *Anas crecca* has its lowest amplified frequency at about 2,400 Hz., with a minor harmonic at 4,800 Hz. and a more intense one at 7,600 Hz. (Figure 3e). By comparison, the female alarm calls of both the Teal and Shoveler *Anas clypeata* have very low fundamental frequencies of under 500 Hz. In the case of the Gadwall these have maximum resonant amplification of harmonics between 2,000 and 3,000 Hz., while in the Teal these are best developed between 2,800 and 3,800 Hz. Greenewalt (1967) reported the fundamental frequency of a female Teal call as 273 Hz., with maximum amplitude in the 12th harmonic at 4,296 Hz.

Inspection of sonagrams of various species of *Anas,* such as those appearing in Frith's book (1967), indicate that similar acoustical characteristics to those of the Mallard female occur in the decrescendo calls of many *Anas* species. Smaller species generally have more rapidly repeated notes and somewhat higher fundamental frequencies, but with little actual change in frequencies throughout the entire call sequence.

A few species of dabbling ducks have male calls that diverge from the typical *Anas* pattern. Several species of the 'blue-winged duck' group lack pure whistles; in the Garganey *Anas querquedula* the male courtship call is a rattling noise produced by broken bursts of 'wooden' sounds having a pulse rate of about 50 per second, somewhat like the rattling sounds of the Mute Swan and the Cereopsis. However, a definite bulla is present in males of this species and of the shoveler group.

In contrast, males of the wigeon group lack *'raeb'* notes and produce only whistled calls. The Chiloe Wigeon *Anas*

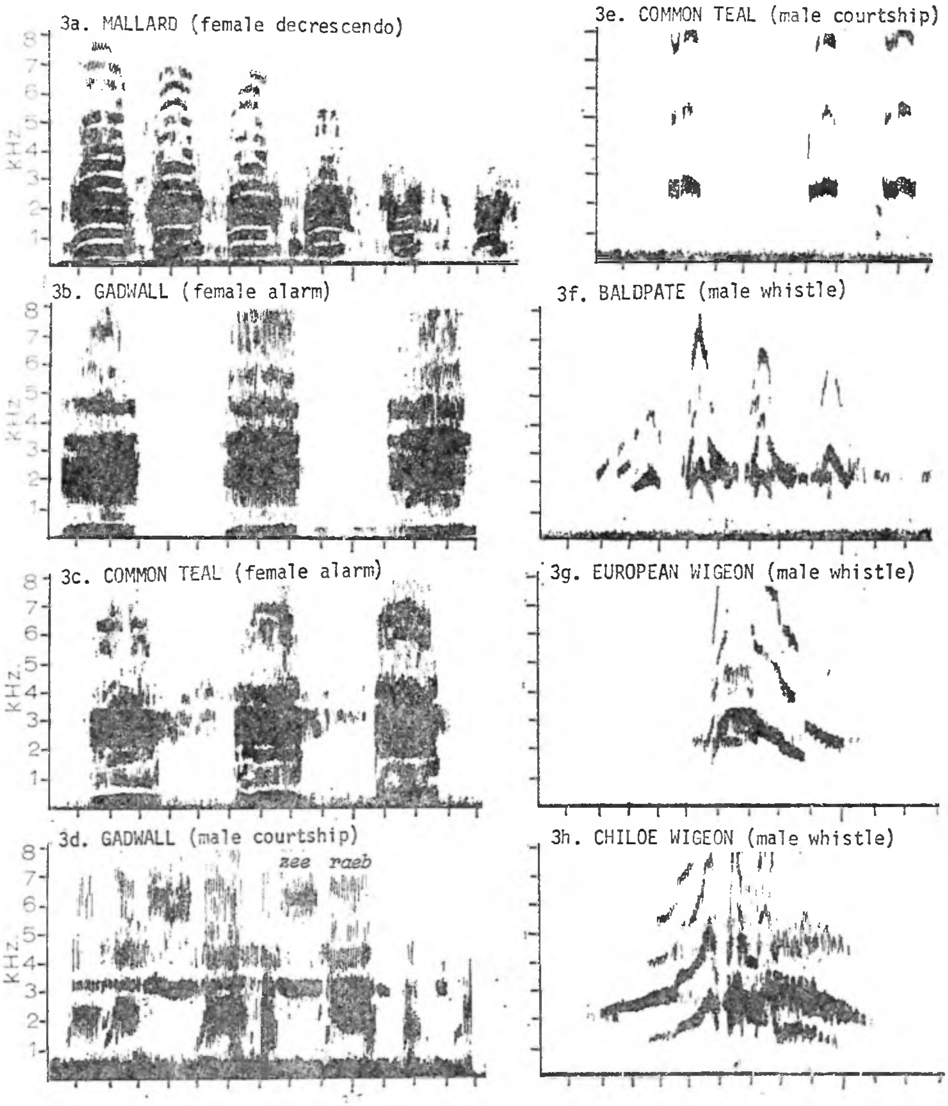


Figure 3. Sonagrams of representative dabbling ducks.

sibilatrix has the loudest calls and the largest tracheal bulla. The American Wigeon *A. americana* has the smallest bulla and the weakest whistles, and the European Wigeon *A. penelope* is intermediate in both regards (Figures 3f-3h). Interestingly, the whistles of the American Wigeon consist of a series of three or four simple ascending and descending notes, with several harmonics and major amplification between 2,000 and 3,000 Hz. The male European Wigeon begins with a weak ascending note, followed by a much louder rapidly ascending note that 'plateaus' in fundamental frequency at about 3,400 Hz. It then gradually drops off in a *glissando* of descending frequency, passing through a zone of increase amplitude at about 2,500 Hz. before dying out completely. Finally, in the Chiloe Wigeon, the call is a nearly continuous flow of sound energy lasting approximately one second. It starts with a rise in fundamental frequency from about 1,000 Hz. to 2,500 Hz., where a *vibrato* effect begins and the call gradually diminishes in amplitude and fundamental frequency. In all three species major amplification occurs in frequency zones around 2,000, 4,000 and 8,000 Hz., which would be best accounted for by a tracheal tube some multiple of 9 cm. long.

Tribe Aythyini (Pochards)

As described previously (Johnsgard 1961), the tracheal anatomy of the pochards is of unusual interest, owing to the variations in the diameter of the tracheal tube of males, and the partially membraneous syringeal bulla. The acoustical functions of both adaptations remain obscure, although it may be presumed that gradually varying tracheal tube diameters would somewhat affect the efficiency of the resonating characteristics of the trachea, whereas abrupt changes in diameter, as in the Rosybill *Netta peposaca*, might have quite different acoustical effects.

Pochard calls are usually both relatively weak in amplitude and low in pitch, and are thus difficult to separate from background noises. The greatest zone of amplification of the male calls available appears to be at or the fundamental frequency, under 1,000 Hz. For example, the courtship call of the male Canvasback *Aythya valisineria* exhibits greatest amplification at about 750 Hz., with minor resonant amplitude two harmonics above at 3,000 Hz., but virtually no harmonic development above that frequency. Female calls show similar amplitude characteristics. By contrast, the male calls of the Redhead *Aythya americana* are more prolonged and have strong amplitude development not only at 750 Hz., but also at 2,200 and 3,000 Hz., and progressively weaker harmonics at higher frequencies. Most striking of all is the male call of the European Pochard *Aythya ferina*, which is unusually prolonged (1.4 seconds) and has remarkable harmonic development. As may be seen on the sonagram (Figure 4a), the call gradually rises in frequency, makes a sudden dip near the middle (compare Chiloe Wigeon, Figure 3h); this is followed by a point of maximum frequency (fundamental frequency ca. 780 Hz.), and is terminated by a gradual *glissando* to the starting point. Individual harmonic bands increase and decrease in amplitude as they pass in and out of zones of resonant frequencies. These appear to be approximately 700 Hz. apart, suggesting a resonating tube length of about 24 cm.

Calls of female pochards are acoustically much like those of female dabbling ducks. Thus, the alarm call of a female Lesser Scaup *Aythya affinis* has the same paced cadence and low fundamental frequency evident in Gadwall, Mallard, and Green-winged Teal. These notes have maximum resonant amplification of harmonics in the zone between 1,900 and 2,900 Hz. (Figure 4c). The inciting notes are acoustically similar (Figure 4b). In the Canvasback at least, inciting calls appear similar to inciting notes of *Anas* females, having wide frequency content and relatively poor harmonic development. Decrescendo calls are virtually lacking in this group (Johnsgard 1965).

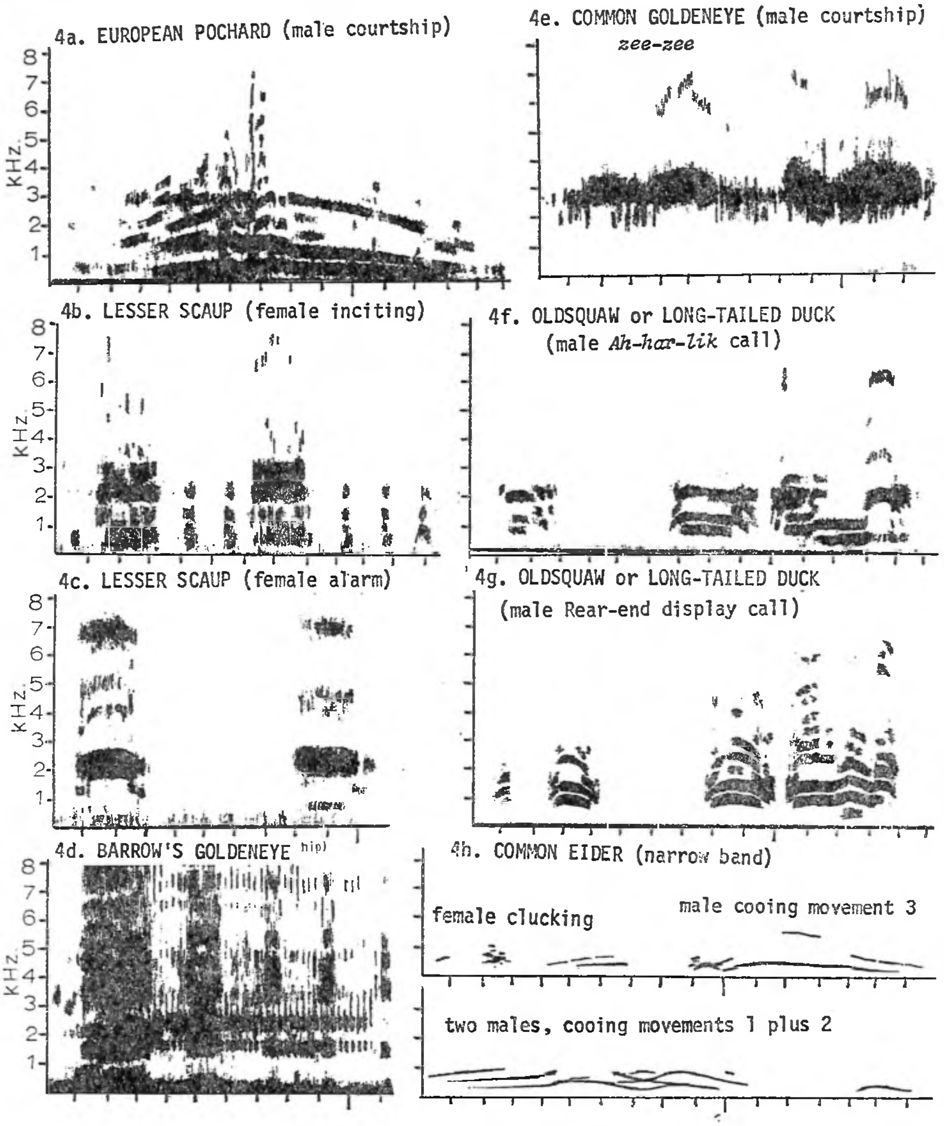
Tribe Mergini (Sea Ducks)

All of the problems posed by the Aythyini are present in the sea ducks, including variably enlarged tracheal tubes, complex and partially membranaceous bullae, enlarged bronchial tubes, and in the case of one genus (*Polysticta*), unusually well developed *sternotrachealis* muscles.

The typical eiders (*Somateria*) provide a special problem. Male vocalizations of all species are low cooing sounds, which involve the inflation of the throat region with air presumably, but not definitely, resulting from inflation of the interclavicular air sac. This would require that the vocalization occurs during inhalation, which is not yet definitely proven for birds but may well occur (Kelemen 1963).

However, sounds of the same 'booming' quality are produced by male Pinnated Grouse *Tympanuchus americanus* by inflation of the oesophagus with air expelled from the tracheal tube. This, in the case of the grouse, has the acoustical effect of adding an expansible chamber to the end of a resonating tube, the greatly increased volume allowing for a more effective resonance of very low frequency sounds.

The 'cooing' sounds of male Common Eiders *Somateria mollissima* certainly support the view that these low frequency harmonics are most effectively amplified. The fundamental frequency appears to be under 600 Hz. even at the call's point of highest pitch, and the lowest frequency band has the greatest amplitude. These low frequencies are best illustrated by a narrow-band filter display on the sonagram (Figure 4h). It is suggested that, whatever the eiders may use as inflatable structures, this behaviour effectively amplifies low frequency sounds, which otherwise would require an open-tube resonator of 35 cm. or longer. Calls of female eiders also have low fundamental frequencies but little harmonic structuring (Figure 4h).


4a. EUROPEAN POCHARD (male courtship)

4b. LESSER SCAUP (female inciting)

4c. LESSER SCAUP (female alarm)

4d. BARROW'S GOLDENEYE hip)

4e. COMMON GOLDENEYE (male courtship)

4f. OLDSQUAW or LONG-TAILED DUCK (male *Ah-har-lik* call)

4g. OLDSQUAW or LONG-TAILED DUCK (male Rear-end display call)

4h. COMMON EIDER (narrow band)

Figure 4. Sonagrams of representative pochards and sea ducks.

The male calls of Long-tailed Ducks (Oldsquaws) *Clangula hyemalis* provide an interesting contrast (Figures 4f and 4g). The rich and penetrating calls have harmonic contents similar to those of some long-necked geese and swans. The fundamental frequency does not vary appreciably; instead there is considerable syllable emphasis and amplitude variation of harmonics that produces a melodic rhythm. The fundamental frequency in the part of the '*Ah-har-lik*' call that has maximum resonating harmonic development is approximately 440 Hz., with the greatest amplitude evident around 2,200 Hz. (Figure 4f). A second zone of well-amplified sounds occurs at about 6,500 Hz. In this loudest part of the call the fundamental frequency is apparently raised from a level that is best amplified at about 1,100 Hz. to an amplification of the next higher resonating frequency. A tracheal length of about 15 cm. would account reasonably well for these two resonating frequencies. A similar call (Figure 4g) with slightly different cadence characteristics, is associated with the 'Rear-end display' (Johnsgard 1965). A better match of fundamental and resonating frequencies may be seen through most of the call. The greatest amplitude is in two harmonics between 900 and 1,800 Hz., which are apparently the first two harmonics above the fundamental frequency, rather than in the fourth or fifth harmonic as evident in the other call. It would seem that only distinctly different degrees of neck-stretching could account for these marked differences in harmonic amplification.

Relatively little can be said about goldeneye (*Bucephala*) calls, other than to note that they appear to have little harmonic structuring. One call from a female Barrow's Goldeneye *B. islandica* has a low fundamental frequency with maximum amplification between 2,000 and 2,500 Hz. One male call, the clicking noise produced during various displays such as the 'Crouch' (Johnsgard 1965), exhibits (Figure 4d) an interesting combination of a simultaneous series of pulsed syringeal noises and an unbroken train of clicks. The clicks are produced at a rate of about 48 per second, while the fundamental frequency of the basic vocalization seems to be around 130-140 Hz. The two sounds seem to be differentially resonated, the strongest amplification of the clicks being at 2,500 Hz., with lesser amplification at 1,700 and 3,400 Hz., whereas the basic vocalization is best amplified at 1,700 and 3,400 Hz. This is in strong contrast to the '*zee-zee*' call of the male Common Goldeneye *B. clangula.* This, in spite of an apparently quite low fundamental frequency of under 1,000 Hz., is strongly amplified between 2,800 and 3,800 Hz., with another minor harmonic zone reappearing between 600 and 700 Hz. (Figure 4e).

Calls of the other sea ducks, such as the mergansers (*Mergus*) and scoters (*Melanitta*), are not available for comment.

Discussion

Sonagrams of calls from species representing most of the major waterfowl tribes clearly support the contention that the tracheal tube is a functional resonator. It appears to act as an open rather than a closed tube, as already concluded by Sutherland and McChesney (1965). Not surprisingly, this resonating ability is most evident in the larger species, for at least two reasons. First, the longer the tracheal tube, the greater the number of resonant frequencies available for matching the fundamental frequency or its harmonics (Figure 5). Secondly, the larger species are more likely to have a syrinx with a fairly large tympaniform membrane area, and thus a lower fundamental frequency; this would allow a larger number of harmonics within the zone of audible sound. In general then, large species would be expected to produce vocalizations with low fundamental frequencies and rich development of harmonics. Short-necked and relatively small species should be more able to produce high-pitched tones with few harmonics, and thus be able better to avoid the 'tuning' effects of the tracheal tube, and have greater abilities for continuous rather than stepped frequency changes during calling.

No clear function for the variations of the tracheal diameter in males of many duck species is yet apparent, but it must be assumed that these affect resonating characteristics of the tracheal tube in some manner. Similarly, it is believed that the function of the bulla in male ducks is to 'emancipate' the male from the tuning effect of the trachea and the low fundamental frequency characteristics of the source-generated (syrinx-produced) calls. If the bulla in fact acts like an aeolian whistle, species specificity in male calls could be readily achieved by varying the size and shape of the male's bulla through genetic and/or hormonal controls (Lewis and Domm 1948) without influencing the basic anatomy of the female's

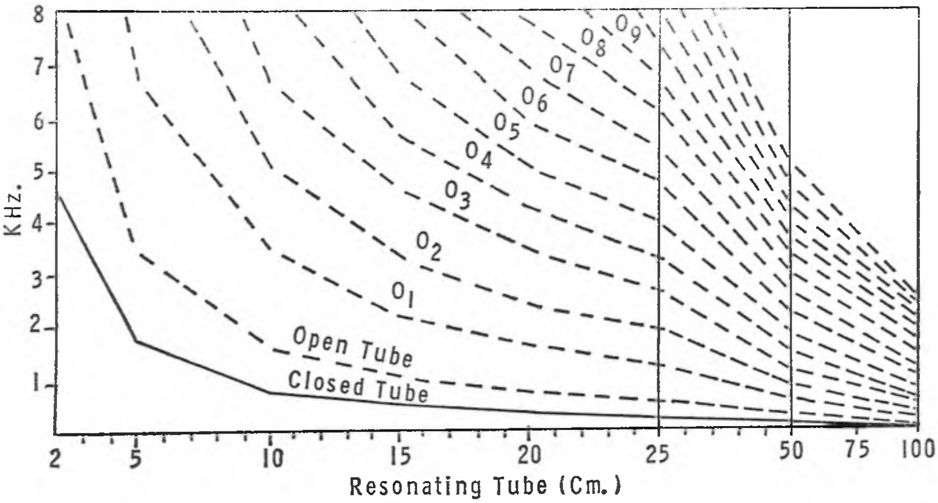


Figure 5. Calculated zones of tracheal resonance (up to 8,000 Hz.) for various tracheal tube lengths, showing the expected resonant frequencies for the first 15 resonant frequencies in an open-tube acoustic system. A closed-tube system would resonate frequencies represented by the solid line and all of its multiples (i.e. the broken lines as well as mid-points between these lines).

syrinx and vocal requirements. Male bullae are poorly developed in very small species such as pygmy geese; here apparently the syrinx is already so small that nearly pure and high-pitched whistled tones can be generated by rapid vibration of the tympaniform membranes. It should be noted, however, that although even downy male ducklings exhibit a bulla, the vocalizations of juvenile birds exhibit no sexual differences (Kear 1968). The whistle-like sounds produced by male ducks are used for the most part in social courtship, although a few species (such as wigeon) have apparently adapted them to all communication functions.

In the eiders, a second and somewhat contrasting vocal adaptation has evidently been achieved by males. The male bulla of these species is quite small and the trachea lacks enlargements, but its effective resonating length is seemingly increased to the point that fundamental frequencies of under 600 Hz. are effectively amplified. Inflation of either the air sacs or possibly the oesophagus during calling is probably responsible.

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Summary

A comparison of inter-species variations in the tracheal anatomy and acoustical characteristics of anatid vocalizations supports the contention that the trachea serves as a resonating tube, thus allowing for differential amplification of the syrinx-generated fundamental sound frequencies and their associated harmonics. The trachea apparently acts acoustically like an open-pipe, rather than a close-pipe, resonating instrument. Species having longer tracheal tubes seem to exhibit a greater degree of tracheal tuning effects and more ability to resonate lower sound frequencies than can species having shorter tracheal tubes. The extreme elongation of some species' tracheal tubes by convolution, as found in the genera *Anseranas* and *Cygnus*, is a functional acoustic adaptation for long-distance communication by low-frequency sounds. The evolution of tracheal bullae by males of most Anatinae species is a method of 'emancipating' the male sex from the relatively uniformly low-pitched and harmonic-rich calls of female ducks. Male courtship calls thus acquire greater species-specificity as well as relatively harmonic-free tones, and are primarily uttered in social situations at short distances.

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