THE VOCAL APPARATUS OF SOME NORTH AMERICAN OWLS

WITH ONE ILLUSTRATION

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Studies of the anatomy and function of the vocal apparatus of owls have not thus far dealt with many of the North American species. Most of our knowledge of strigine syringes is based on Beddard's dissections (1888 and 1898) of scattered representatives of the group, chiefly from the Old World. In examining syringes of eight species of owls from the western United States I have encountered, firstly, some sex differences which are correlated with differences in the utterances of the birds, and, secondly, some facts decidedly at variance with Beddard's descriptions and illustrations. These matters and the functioning of the apparatus appear to merit clarification. I am indebted to Miss Frances Carter, Mr. Lawrence V. Compton, Dr. Loye Miller, Dr. S. B. Benson, and Mr. W. H. Behle for aid in securing materials.

The syringeal enlargement of the air passages of owls occurs chiefly in the bronchi where the latter join with the trachea. The enlargement is effected by increased diameter of the cartilaginous, sometimes partly osseous, rings. At the point of enlargement the rings are much more rigidly bound together than posteriorly along the course of the bronchi. In this way they form on each bronchus a fairly rigid sound chamber well set off from the remainder of the bronchus. The rigidity of structure extends forward through the first few rings of the trachea, but little enlargement is to be noted here in comparison with the remainder of the trachea.

The bronchial rings of the syrinx are incomplete dorsomedially, their free ends joining with those of adjacent rings to form well defined margins. Across the space between these margins is stretched a thin membrane like the head of a drum (internal membrana tympaniformis). The membrane is bounded anteriorly by the fusion of cartilages at the junction of the bronchi. Posteriorly it is continuous with a lesser, narrower membrane extending on down the bronchus. The cartilaginous bar that runs dorsoventrally and marks the beginning of the division of the single tracheal passageway into the bronchial chambers is the pessulus. No discernible vibratile semilunar membrane extends anteriorly from the pessulus, the pessulus merely bearing a sharp anteriorly projecting edge. I have been unable to find any internal muscle fibers in this immediate region.

Owls are uniform in the possession of a single pair of intrinsic muscles that run on either side of the vocal apparatus from the lower trachea to the bronchial ring just posterior to the solid block of bronchial rings comprising the main syringeal sound chamber. The principal point of variation among members of the group is the length of the bronchial enlargement. Another way of expressing this variation is in terms of the number of the ring to which the intrinsic muscle attaches.

In this connection should be mentioned a confusion in the terminology of the rings owing to various views regarding the termination of the trachea. The viewpoint I prefer is to consider the most posterior ring with which the pessulus merges as the last tracheal ring. (The pessulus may merge on the dorsal side only with the penultimate tracheal.) This usage presupposes, in making comparisons, that the location of the pessulus is constant and homologous throughout the group. The other viewpoint is to regard the muscle insertion as a constant point of reference and term the ring involved in the insertion the first bronchial ring. The varying number of rings anterior to it are then termed incomplete or divided tracheal rings—a rather ambiguous designation. By this latter method it is implied that the trachea has split into two tubes

which one might call false bronchi. I am aware of no good evidence in owls for considering the region just posterior to the bifurcation in this light. Perhaps neither the muscle attachment nor the pessulus are homologous in their loci throughout the owls. But, in view of observed differences in the two sides of a single individual as to point of muscle insertion, I regard this as the least stable and hence least useful point of reference.

The muscle attachment criterion seems to be used justifiably by Forbes (1882) in his treatment of the Tubinares. Beddard in his earlier paper on owls (1888) used the muscle insertion as point of reference, but abandoned it for the other criterion in his Structure of Birds (1898). This change I believe to have been responsible for an erroneous statement in the latter paper. Beddard reports that the point of muscle insertion (length of bronchial syrinx) varies from bronchial ring number one in *Tyto alba* (*Strix flammea* of Beddard) to number ten in *Asio* (*Scops* of Beddard) *leucotis*, an African species. My own dissection of *Tyto alba pratincola* showed the rings much fused and the insertion apparently on the third bronchial ring, possibly on the second, but certainly not the first (numbered from the pessulus); Beddard's finding is clearly indicated in a drawing supplementing his description. His statement (1898, p. 252) that the insertion is on the first bronchial in *Bubo* and *Syrnium* (*Strix*) is not borne out by his drawing of *Bubo maculosus* which shows it at least as far distal as the third ring. This discrepancy which I have indicated seems due to faulty transcribing from one system of ring numbering to the other. My examinations of a number of syringes of *Bubo virginianus* and of *Strix occidentalis* reveal insertions on the fourth to sixth rings. *Asio wilsonianus* (*Asio otus wilsonianus* of Hartert) has insertions on the sixth, seventh and eighth rings; Beddard reports insertion on the seventh in *Asio otus*. His drawing of *Asio leucotis* indicates the eighth or ninth ring rather than the tenth as reported.

The extreme of development as regards numbers of rings in the sound chambers which I have found has been in *Otus asio* and *Cryptoglaux acadica* where the insertion is on the eighth bronchial. In *Asio wilsonianus* the bronchial rings were not complete as Beddard found to be the case in *Asio leucotis* and the European *Asio otus*, a significant difference in Old World and North American Long-eared Owls. Both Beddard and Wunderlich (1886) did not find complete bronchial rings in *Asio flammeus* (formerly *A. brachyotus*).

Tabular presentation of the insertions and of the width across the entire apparatus from the insertion on one side to that on the other follows. The latter indicates the general proportions of the apparatus so that comparison with body weights of these and other owls may be made.

Number	Name	Sex	Muscle insertion Right	Left	Width in mm. across points of insertion	Weight in grams
62757 M.V.Z.	Tyto alba pratincola	♀	3	3	7.0	530.0
1373 L.V.C.	Tyto alba pratincola	♂	3	3	6.3	....
1269 A.H.M.	Strix occidentalis caurina	♀	5	4	8.4	....
1729 A.H.M.	Strix occidentalis occidentalis	♂	6	5	10.5	528.1
1271 A.H.M.	Strix occidentalis caurina	♂	6	5	11.8	....
31270 M.V.Z.	Strix occidentalis caurina	♂	..	..	..	610.0
25887 M.V.Z.	Strix occidentalis occidentalis	♀	..	..	..	693.0
62738 M.V.Z.	Bubo virginianus pacificus	♀	5	5	15.0	1544.3
61345 M.V.Z.	Bubo virginianus occidentalis	♀	5	5	15.2	....
63665 M.V.Z.	Bubo virginianus saturatus	♂	5	5	17.3	....
62653 M.V.Z.	Bubo virginianus pallescens	♂	5	5	17.8	....
62739 M.V.Z.	Bubo virginianus pacificus	♂	5	5	18.0	1010.0
64071 M.V.Z.	Bubo virginianus pallescens	♂	5	5	19.2	....

62758	M.V.Z.	Bubo virginianus pacificus	♂	5	5	19.5	1083.0
27881	M.V.Z.	Speotyto cunicularia hypugaea	♂	..	..	..	143.7
1227	L.V.C.	Speotyto cunicularia hypugaea	♂	6	6	7.0	....
1708	A.H.M.	Glaucidium gnoma californicum	♂	6	5	5.7	61.1
1532	A.H.M.	Glaucidium gnoma pinicola	♂	5	6	6.3	61.0
1649	A.H.M.	Glaucidium gnoma californicum	♂	6	6	6.2	....
1732	A.H.M.	Asio wilsonianus	♀	7	6	8.1	209.7
64073	M.V.Z.	Asio wilsonianus	♂	7	8	9.0	196.3
63664	M.V.Z.	Cryptoglaux acadica acadica	....	8	..	6.6	....
1229	L.V.C.	Otus asio asio	♀	8	8	6.8	....
62618	M.V.Z	Otus asio gilmani	♂	8	7	7.7	....
1684	A.H.M.	Otus asio gilmani	♂	8	8	7.5	....
51738	M.V.Z.	Otus asio quercinus	♀	..	..	. ..	163.2
53765	M.V.Z.	Otus asio quercinus	♀	..	..	..	164.0
51737	M.V.Z.	Otus asio quercinus	♂	..	..	..	131.5
31050	M.V.Z.	Otus asio quercinus	♂	..	..	..	108.0

The asymmetry in the number of rings in the bronchial syringes of *Strix occidentalis, Asio wilsonianus, Glaucidium gnoma* and *Otus asio*, considering the small number of specimens of each examined, points to high frequency of occurrence of this asymmetry; whereas, the perfect symmetry in seven specimens of *Bubo virginianus* suggests lack of asymmetry in this latter form. When the two bronchial sound chambers are unequal, the right side is not always greater than the left, the reverse being true in one of the Pigmy and one of the Long-eared owls. Asymmetry is always brought about by the addition or subtraction of rings from the rigid block of rings constituting the sound chamber, not by the insertion of an extra loose ring just anterior to the muscle attachment. Actually the difference in number of rings overemphasizes the asymmetry, since an extra ring is partially compensated for by lesser width of rings on the side on which it occurs.

Such variation in component elements of right and left sound chambers and the variation among individuals shown in the table make it clear that the point of muscle insertion, which varies in accordance with the sound chamber, is not sufficiently stable to be used as a starting point for numbering the rings of the air passageways. Should one follow the muscle insertion criterion and consider this point the end of the trachea, it is impossible to explain the rings of asymmetrical sound chambers as divided tracheals; unequal numbers of rings on the two sides could hardly be produced by a median division of each tracheal.

The asymmetry of the syrinx, so far as I am aware, has not been detected in owls heretofore, although various types of asymmetry are well known in other orders of birds. The condition is of especial interest in this group, because of the well known occurrence of ear, and concomitant skull, asymmetry in the Strigidae. Of the four types in which I have found asymmetrical syringes, *Glaucidium* and *Otus* are without asymmetry of the ear; *Strix* and *Asio* have asymmetrical ears. *Bubo*, according to Shufeldt (1900) in his translation of Collett, is asymmetrical in the ear region, while Coues (1903) considers it symmetrical. The asymmetries of syrinx and auditory apparatus are, then, not necessarily associated, yet the tendency to asymmetry within the family is more strongly established by these data on the syrinx. Possibly there is some significance in the fact that Collett found the right ear more often the larger of the two, just as I have found the right bronchus more frequently to possess the greater number of rings. There are six of the eight asymmetrical syringes in which the right side has the greater number of rings. Is there possibly a deep-seated predilection to morphological dominance of the right side?

The differences in the syringes of the species I have dissected do not indicate, I believe, any special relationships between these forms and do not place them in a sequence that is in agreement with the relationships indicated by other characteristics

of the species. *Asio wilsonianus* differs from others by reason of a broadly flattened anterior margin of each sound chamber. Wunderlich (1886) apparently found the same condition in *Asio flammeus*. Even the Barn Owl, for other reasons known to be well set off from the Strigidae, as regards syrinx represents little more than one extreme of the more or less continuous structural series; it is not widely separated from *Strix* in the number of rings, although the rings are more completely fused, and the two short sound chambers are bound together medially by a ligament. Beddard likewise was unable to attach much phylogenetic significance to owl syringes.

Among birds generally, sex differences in the syrinx are not uncommon. Such differences are pronounced in ducks and have been reported in several gallinaceous forms and in song birds. Appel (1929) recently has found, however, that in the brown leghorn structural differences are lacking. According to Häcker (1900) song birds display a sex dimorphism manifested as weaker muscles and less specialized cartilages in the female. When females have been heard singing in a manner comparable to males, it is often reported that their songs differ from those of the males in volume, not in pitch or complexity. The similarity is not so perfect, however, in many oscine species, as for example in *Icterus* where differences in song pattern and quality have been detected (Miller, 1931, and Youngworth, 1933).

In 1930 Loye Miller described sex differences in Horned Owl notes, a condition familiar to several persons who have listened to and collected Horned Owls but apparently not recorded in print by many writers. My own observations of Horned Owls have determined an average difference of three, sometimes four, half tones of pitch, the males being the lower. Comparable intervals probably distinguish male and female Screech Owls. An individual Horned Owl has been known to alter the pitch of its hoot, within a few minute's time, a matter of two half tones. Nevertheless, the average difference between the sexes is so marked that in the field one may with practice fairly satisfactorily identify them by this means.

I have no data on sex differences in the voices of Burrowing, Pigmy, Long-eared and Barn owls, but with regard to the Spotted Owl I offer the following experience. On May 26, 1932, fourteen miles west of Willits, Mendocino County, California, I called into camp a pair of Spotted Owls. One bird hooted consistently five to six half tones higher than the other. In the assortment of barks, whistles, and cat-calls in which this species is proficient, I could not distinguish comparable differences, but the hoots were always differentiated. The male was collected just after it was watched in the beam of a flashlight giving the low-pitched hoot. The other bird of this pair (without doubt a female in view of the season and joint occupancy of a territory with the male) was not secured; but another female was taken on the same expedition on the Eel River, ten miles north of Garberville, Humboldt County.

Turning attention again to the Horned Owls where the sex difference is best known, it may be seen from the measurements in the table that the females possess smaller syringes, this despite the fact that females are much larger birds than males. Available figures show that females weigh about 50 percent more than males. Contrarily, the syringes (using the aforementioned measurements as an index) of females average 17 per cent smaller than those of males. The single female Screech Owl syrinx is 10 per cent smaller than those of males; body size of females is about 33 per cent greater. The female Long-eared Owl has a syrinx 10 per cent smaller and weighs 7 per cent more than the male.

The sexes in *Strix occidentalis* are not as greatly differentiated in body size and wing length (see Oberholser, 1915, p. 255) as in *Bubo* and *Otus,* though the female is here also the larger. It perhaps follows, then, that the one available female syrinx

is relatively extremely small, being 24 per cent less than the average of the two males (see fig. 37). Not only is it small but it also possesses fewer bronchial rings as is the case in the female *Asio*.
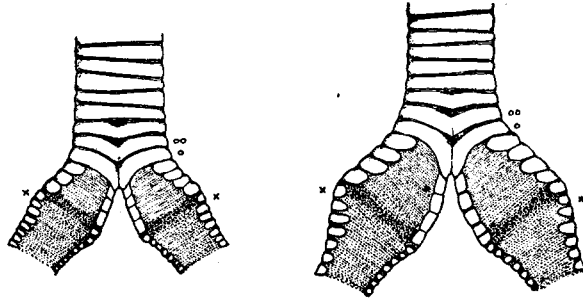

Fig. 37. Dorsal view of syringes of *Strix occidentalis*, × 2½; left, female, no. 1269 A.H.M.; right, male, no. 1271 A.H.M. Letter x marks ring on which intrinsic muscle inserts; o = last tracheal ring; oo = penultimate ring. Thickened portion of internal membrana tympaniformis is represented extending across between ends of cartilages at point of muscle insertion. Note sexual dimorphism in size and number of rings, and asymmetry of bronchial sound boxes.

Tyto alba differs markedly from the foregoing inasmuch as the female syrinx is 11 per cent greater than the male.

It may be concluded that syringeal size in certain, and perhaps all, of the Strigidae is a well-marked secondary sexual character that reverses a trend in general bodily development which would, *a priori*, lead one to anticipate a larger voice box in females as appears to be the case in the Barn Owls (Tytonidae). The structures are not only different quantitatively but are responsible for average differences in pitch of hoots. The smaller syringes are obviously productive of the higher tones. It does not seem likely that nervous control would account for all difference in pitch; rhythm is more liable to differential nervous control in the sexes. The situation may be compared to the sexual differentiation of the human larynx and voice but not carried to so great a degree.

To attempt to locate more exactly the parts responsible for the pitch of an owl's hoot, I attached the two bronchi of a freshly killed Horned Owl's syrinx to glass tubes carrying compressed air. The only manner in which a sound could be induced was by spreading the bronchi so that the bronchial tubes were constricted at the posterior end of each voice box and the air thrown against the dorsomedial membranes of the boxes. Gratifyingly, the sound produced was similar to a Horned Owl hoot in pitch and in many points of quality, although it lacked greatly in resonance and volume. It was sufficiently similar that I am convinced the vibration of the membrane which I could clearly see was intimately connected in some way with the initial vibration and fundamental tone of the normal hoot. The complicated screeches and whistles of Spotted, Screech and Long-eared owls might be initiated in the syrinx in a different manner. In the experiment the entire trachea was intact. When finally the trachea was broken shortly in front of the syrinx much of the quality of the note was lost owing, I presume, to loss of resonance for the overtones as well as for the fundamental, but the pitch of the fundamental remained unchanged.

These observations prompted further inspection of the membranes of the bronchial sound boxes. The internal membrane opposite the ring on which the muscle inserts was found to be slightly thickened and the parts of the membrane next the free ends of this incomplete ring bore a layer of muscle internally. Also at this point on the other side of the tube just behind the ring bearing the insertion and between it and the next ring posterior there is a considerable extent of loose membrane (external membrana tympaniformis) which unless the intrinsic muscle be contracted projects as a fold or pocket into the cavity of the passageway. When the extrinsic muscles contract the whole syrinx is thrust back toward the sternum. This throws the bronchi more nearly at right angles to the trachea and bends the bronchi at the ends of the sound chambers. The angle at this point causes the fold of the external membrane to project far into the cavity almost or entirely in contact with the opposite, internal, membrane. In this position air can vibrate the membranes, particularly the internal membrane as witnessed in the experiment. The muscles on the membranes should be able to regulate tension. Tension may also be modified by the changes in the position of cartilages induced by intrinsic and extrinsic muscles. Contraction of the intrinsic muscle withdraws the fold of the external membrane from the passageway so regulating the aperture. It may be that vibration is set up in the external membrane which bears some resemblance to the mammalian vocal cord as well as in the opposite membrane.

The frequently encountered statement regarding function of the avian syrinx ascribes the sound to vibrations of the semilunar membrane on the pessulus. This is true of singing birds, but in many others the vibrations are set up in loose membranes between bronchial or tracheal rings or by a membrane such as I have described in owls. In chickens tympanic membranes on the lateral and medial surfaces of the syrinx between widely separated rings vibrate to produce the tone (Myers, 1917). I have traced sound in a turkey syrinx to a similar source by using compressed air as was done with the Horned Owl. No functional semilunar membrane is present in these Galliformes.

At the time these investigations were conducted I was not aware of the recent paper by Rüppell (1933) which treats in admirable fashion of the physiology and acoustics of the syrinx. My findings accord with his, namely, that the tone is produced by vibrating elastic membranes of the syrinx setting up vibrations in the column of air passing through the trachea. The mechanism is to be compared with an organ pipe (reed type). It is not perhaps certain, however, to what degree the period of vibration of the membranes is influenced by the length of the trachea acting as a resonator. Working experimentally with hens and with a crane syrinx Rüppell found, as did Myers (1917), that shortening the trachea raised the pitch, presumably because the resonator (trachea) is gaged then to a shorter wave length and the membrane coerced to vibrate in accordance with that length. Rüppell's results leave little doubt on this point on the species investigated. In owls I am inclined to believe the membrane acts as a driver, to use Negus' description (1929), and sets up a given vibration rate whether the tracheal tube resonates the fundamental or not. In such case the membrane sets its own pace and is not altered by length of its pipe. I have been brought to this viewpoint regarding owls because the pitch was not altered when the trachea was shortened and because female owls, although possessing tracheae equal to or longer than those of males, produce sounds of higher pitch.

Even where tracheal length influences the pitch it is not certain that the individual bird varies the length to alter the pitch; rather is this done, in part at least, by varying tension in the membranes. Reference to figure 37 will show that the bron-

chial voice boxes of owls are widest at the posterior end exactly where the vibratile membranes are situated. The width taken here across the ends of the cartilage rings will be essentially the length of the vibrating membranes. Length of membrane is important, for, if tension is constant, length of membrane is inversely proportional to vibration rate or pitch, presuming that tracheal length does not dictate vibration rate of membrane. A thin rubber band of length equivalent to the elastic membrane of a Horned Owl syrinx when placed at low tension can be blown upon to emit a tone near that of the pitch of the bird's hoot. Lengths of membranes in millimeters, with diameters of bronchi behind syrinx and tracheae in front of syrinx as standards of comparison, follow:

Number		Species	Sex	Length of vibrating membrane	Per cent of bronchial diameter	Bronchial diameter	Tracheal diameter
62757	M.V.Z.	Tyto alba	♀	7.0	166	4.2	5.8
1373	L.V.C.	Tyto alba	♂	6.7	167	4.0	5.8
1269	A.H.M.	Strix occidentalis	♀	7.1	191	3.7	4.6
1271	A.H.M.	Strix occidentalis	♂	8.4	227	3.7	5.6
1729	A.H.M.	Strix occidentalis	♂	8.8	209	4.2	5.9
61345	M.V.Z.	Bubo virginianus	♀	11.1	209	5.3	7.7
62738	M.V.Z.	Bubo virginianus	♀	12.0	203	5.9	8.6
62653	M.V.Z.	Bubo virginianus	♂	12.3	223	5.5	7.6
62739	M.V.Z.	Bubo virginianus	♂	12.4	238	5.2	8.6
64071	M.V.Z.	Bubo virginianus	♂	12.9	......	....	8.3
63665	M.V.Z.	Bubo virginianus	♂	13.3	221	6.0	8.7
62758	M.V.Z.	Bubo virginianus	♂	13.7	228	6.0	9.0
1227	L.V.C.	Speotyto cunicularia	♂	5.7	203	2.8	4.4
1708	A.H.M.	Glaucidium gnoma	♂	3.6	......	....	2.5
1532	A.H.M.	Glaucidium gnoma	♂	3.8	211	1.8	2.7
1649	A.H.M.	Glaucidium gnoma	♂	3.9	205	1.9	3.0
1732	A.H.M.	Asio wilsonianus	♀	6.4	200	3.2	4.6
64073	M.V.Z.	Asio wilsonianus	♂	7.3	214	3.4	4.5
63664	M.V.Z.	Cryptoglaux acadica	....	4.0	......	....	3.3
1229	L.V.C.	Otus asio	♀	4.2	190	2.2	3.9
1364	A.H.M.	Otus asio	♂	4.7	204	2.3	3.8
62618	M.V.Z.	Otus asio	♂	5.0	......	....	3.9

My own observations indicate that the pitches of male owls' hoots in certain species average as follows: *Bubo virginianus*, D (immediately above middle C); *Strix occidentalis*, C¹ (an octave above middle C); *Otus asio gilmani*, F¹; and *Glaucidium gnoma*, A#¹. The reader should be reminded that the lesser resonance and volume in the smaller owls gives to an uncritical ear the impression of greater differences in pitch than actually exist. The hoot of *Strix occidentalis* commences on C¹, but the terminal note slurs down to about F#.

If 12.9 mm. be taken as the length of the membrane in male Horned Owls and D the tone produced (287.4 vibrations per second in the tempered scale) we can calculate what the hoots of males of the other species should be if the tone is a simple membrane vibration with tension and elasticity constant. Proceeding with the calculation, the vibration rate for *Strix occidentalis* is 442 or near A about half way between the observed top note and terminal slur. The figure for the Screech Owl is 764 or about G¹, one full tone higher than observed average. That of *Glaucidium gnoma* is 950 or between A#¹ and B¹, a little less than a half tone higher than observations. In the matter of sex differences, the female Horned Owls should hoot near 321 or E which is a full tone higher than males, the observed difference being usually three half tones. In the Spotted Owl the female figures C# or four half tones higher than the male with the observed interval five to six half tones.

The parallelism of membrane length and observed tones, despite imperfections, is apparent. When a number of variables and errors come into the picture, such as

nervous control, error in measurement, varying tension and elasticity of membranes and resonating facilities, it is almost surprising that membrane length and pitch of hoot are so closely correlated. Seemingly different species of bubonid owls hoot in much the same fashion, so that membrane length is an index to the mean pitch value of the fundamental of the hoot.

Having established the significance of the membrane length, this dimension which represents the diameter of the greatest enlargement of the bronchus should be compared with the diameter farther posterior where the undifferentiated tube functions simply for the passage of air. The table gives the diameter at the membrane in per cent of undifferentiated bronchial diameter. The striking fact to be gained from these figures is that in both small and large species of owls the syrinx has been enlarged relative to the bronchus to about the same degree. *Bubo* has a slightly greater enlargement in both sexes, but the difference compared to other species is not striking. Irrespective of species in the Strigidae, female syringes are enlarged to about 160 to 200 per cent, males 200 to 240 per cent. Diameters of tracheae and bronchi of males and females are approximately equal and do not reflect in the data available the greater body bulk of the females. But, the enlargement to provide for the vocal membranes obviously is not equivalent in the sexes. In *Tyto* the enlargement is equivalent in the sexes and equal in degree to females in the Strigidae.

Within one sex, then, with the bronchial enlargement roughly equal in all species, the actual membrane length will vary in proportion to the diameter of the bronchus. Why is it that a Horned Owl has a bronchial diameter and vibratile membrane only three times as great as a Pygmy Owl when its total bulk (weight) is sixteen to twenty times as great? The reason is apparent when it is recalled that the area of the bronchial cross-section rather than the diameter stands in direct relationship to the bulk. The area of cross-section is directly proportional to the air carrying capacity of the bronchi, neglecting friction.

Average areas of cross-section follow: *Tyto alba,* 13.2 sq. mm.; *Strix occidentalis,* 11.7; *Bubo virginianus,* 24.6; *Asio wilsonianus,* 8.0; *Speotyto cunicularia,* 6.1; *Glaucidium gnoma,* 2.6; and *Otus asio,* 4.0. From these it is seen that functionally the bronchi of *Bubo* instead of being three times larger are nearly ten times greater than *Glaucidium.* The areas of bronchial sections approximate *roughly* the bulk of the body. *Bubo virginianus* is about twice as heavy as *Strix occidentalis* and has twice the bronchial section. The smaller owls do have greater bronchial sections relative to weight; this possibly is owing to the greater friction on the walls in these smaller tubes.

In conclusion, the size of the air passages corresponds in general to body size. Increase in body size increases proportionately bronchial cross-section. Diameter of bronchi increases, however, only as twice the square root of the cross-sectional area divided by Pi. Since the vibratile membrane is proportional to bronchial diameter, being in effect equal to the diameter of the enlarged tube, pitch of hoot relative to the size of the owl is much higher in the larger species. In other words, sizes of syringes and the ranges in pitch which they are capable of producing are largely determined by the size of the bird modified by the ratio of diameter of bronchial pipe to area of cross-section, except as altered by sexual differentiation in degree of bronchial enlargement.

SUMMARY

Syringes of eight species of North American owls have been dissected and compared with Beddard's descriptions of Old World species. Structural differences among species appear to have little or no phylogenetic significance, except in the case of *Tyto*

wherein lack of sex dimorphism, ligamentous connection of bronchi and fusion of carti-laginous parts set it apart from other owls.

An asymmetry has been found in the vocal apparatus which is present in certain species but not necessarily in those with ear asymmetry.

Structural differences have not been found that account for different types (qual-ities) of calls in different species. These must be ascribed to nervous control and to other factors influencing the overtones. However, correlation of mean pitch of the principal note (hoot) of several species and size of vocal apparatus has been established.

Sexual dimorphism in the syringes of the Strigidae reverses the trend of differ-entiation in the remainder of the body so that females possess smaller syringes than males (at least in *Bubo, Otus, Asio* and *Strix*). Correspondingly, female hoots are higher. Observed pitches of hoots of several species are recorded.

Experimentation has shown that the sound (hoot) is produced in owls not by a semilunar membrane but by membranes in each bronchus at the posterior end of the sound chambers. Muscular control of the membranes and adjacent parts is described. The tone production mechanism is to be compared to a reed organ pipe in accordance with Rüppell's (1933) views, except that variations in tracheal length seem not to alter pitch. Lengths of vibrating membranes are, in essence, inversely proportional to observed pitches of hoots.

The enlargement of the syrinx proportional to the remainder of the bronchus is closely similar in all species of owls. The higher pitched voices relative to body size in the larger forms seem to be explicable in terms of simple geometric principles governing the ratio of diameter to area of cross-section of the bronchial tubes.

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THE CLASSIFICATION OF SOME AMERICAN PIGEONS

By JAMES L. PETERS

In part 7 of the Birds of North and Middle America, Ridgway gives a key to the American genera of Columbae (pp. 279-283). In page 281 appears the following:

d. Wings more or less spotted with black, the distal coverts not white.
    e. Rectrices 14; the tail more than three-fifths as long as wing; tarsus less than one-sixth as long as wing; bill not decurved; smaller wing-coverts immaculate; a black subauricular spot, but no pale auricular stripe.
        f. Tail longer and more graduated (nearly three-fourths as long as wing to longer than wing)..*Zenaidura*
        ff. Tail shorter, rounded rather than graduated (less than two-thirds as long as wing)..*Zenaida*
    ee. Rectrices 12, the tail less than three-fifths as long as wing; tarsus nearly one-fifth as long as wing; bill decurved; smaller wing-coverts spotted or streaked; no subauricular spot, but a pale auricular band margined above and below by a black line)..*Nesopelia*
dd. Wings immaculate, the distal coverts white..*Melopelia*

The species included under each of these genera as given in the text, including extralimital (South American) forms mentioned in keys and footnotes by Ridgway, are:

Zenaidura macroura macroura (Linn.)
Zenaidura macroura clarionensis Towns.
Zenaidura macroura carolinensis (Linn.)
Zenaidura macroura marginella (Woodh.)
Zenaidura macroura tresmariae Ridgw.
Zenaidura graysoni Lawr.
Zenaidura yucatanensis Lawr.
Zenaida zenaida zenaida (Bonap.)
Zenaida zenaida lucida Noble
Zenaida zenaida yucatanensis Salvad.
Zenaida spadicea Cory
Zenaida aurita (Temm.)
Zenaida ?plumbea Gosse

Zenaida auriculata Des Murs
Zenaida ruficauda ruficauda Bonap.
Zenaida ruficauda robinsoni Ridgw.
Zenaida ruficauda vinaceorufa Ridgw.
Zenaida ruficauda jessiae Ridgw.
Nesopelia galapagoensis galapagoensis (Gould)
Nesopelia galapagoensis exsul Roths. and Hart.
Melopelia asiatica asiatica (Linn.)
Melopelia asiatica mearnsi Ridgw.
Melopelia meloda (Tschudi)

This list is given here in full, partly for convenient reference and partly for the purpose of having it readily available for comparison with the proposed rearrangement to be found at the end of this article.

An examination of the various forms listed in an effort to "work" the key shows