LITERATURE CITED

ALLEN, ARTHUR A. 1930. The book of birds. (D. Van Nostrand Co., Inc., New York), p. 118.

COOKE, MAY THACHER. 1929. Birds of the Washington, D. C. Region. Proc. Biol. Soc. Wash., 42: 1–80.

KENDEIGH, S. CHARLES. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Dept. Lands and Forests, Ontario, Canada, Biol. Bull. No. 1: 31–34.

MOFFAT, C. B. 1903. The spring rivalry of birds. Some views on the limit to multiplication. Irish Naturalist, 12: 59.

NICE, MARGARET M. 1937. Studies in the life history of the Song Sparrow I. Trans. Linn. Soc. New York, 4: 86–87.

STEWART, ROBERT E., AND JOHN W. ALDRICH. 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. Auk, 68: 471–482.

THOMPSON, W. R. 1930. The biological control of insect and plant pests. (Publ. Empire Marketing Bd. 29, H. M. Stationery Office, London), pp. 55–71.

TRAUTMAN, MILTON B. 1940. Birds of Buckeye Lake, Ohio. Misc. Publ. Mus. Zool., Univ. Mich., No. 44: 1–466.

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SOUND PRODUCTION IN PASSERINE BIRDS

BY MILDRED MISKIMEN

IN spite of widespread popular and scientific interest in the singing of birds there is some difference of opinion with regard to the actual functioning of the vocal organ, the syrinx. The British writers, Thomson (1923) and Parker and Haswell (1940) regard the semilunar membrane as the actual sound-producing organ. Miller (1947) by experimental methods determined that in owls and some other birds sound is produced by "the vibrations—set up in loose membranes between bronchial and tracheal rings" but he ascribes the sound produced by singing birds to vibrations of the semilunar membrane. Stresemann (1934), however, asserts that in passerine birds the vibrations produced by air passing over the tympaniform membranes produce the sounds heard in song, and that in song birds the intrinsic syringeal muscles regulate the tensions of these membranes. Cole (1945) in his writing accepts the opinion of Stresemann. The purpose of this study was first, to determine by experiment the way in which sound is produced in passerine birds, and second, to determine whether the structure of the syrinx correlates in any way with the quality of the song.

ACKNOWLEDGMENTS

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THE SOURCE OF SOUND

The semilunar membrane is located inside the trachea on the cephalad edge of the pessulus, marking the beginnings of the bronchial tubes. If air passing over it produces sound after the manner of air passing across the reed of a clarinet, then sound must be produced while air is entering the bird's lungs, which is the relaxed or "passive phase" of respiration in birds. In mammals, as we know, voice is produced during exhalation, which in them is the "passive phase." Thomson and other writers have stated, however, that voice in birds is produced during the "active phase" of respiration, that is, while the muscles of the thorax are forcing air from the lungs. These were points to be tested experimentally.

A common rubber ear syringe was used in this part of the work. The syringe was applied to the severed end of the trachea of an anaesthetized English Sparrow, *Passer domesticus*, and air was forced through the respiratory tubes in alternating directions by compressing and releasing the bulb.

No sound was produced by forcing air into the trachea, but when the bulb was released and air drawn back into the bulb the bronchial tubes partly collapsed and a chirping noise was made. The internal tympaniform membrane just above the insertions of the bronchidesmus membrane on the first bronchial half-rings vibrated freely and rapidly in the inter-bronchial space. These vibrations could easily be seen by placing the bird on the stage of a binocular microscope during the operation. Normally, tension seems to be maintained by the rigidity of the bronchial half-rings, while the relaxation of the membranes due to the difference in internal and external air pressure permitted the vibrations. This agrees with the observations of Miller in his study of owls (1947).

The next step was to force air out through the syrinx by pressure from within. A small hole was made in the abdominal air-sac at the end of the sternum, into which the tip of a medicine dropper was inserted tightly and the rubber syringe fitted snugly into the other end of the dropper. Air could be forced into the air-sac and out through the trachea, producing sound like that produced by drawing air out from the tracheal end. Considerable pressure had to be applied before the sudden, loud chirp was heard.

Drawing air into the air-sac by releasing the bulb produced no sound. It was thought that the intervening air passages through the lungs might interfere with the free passage of air under sufficient pressure and that suction applied directly to the bronchial tubes might produce some sound. As the bronchial tubes of the sparrow are so fine that no effective way to do this could be devised, a Ring-necked Pheasant, *Phasianus colchicus*, was used for this part of the experiment, since its bronchii are larger. Sound was produced when air was drawn outward through the trachea, but not when drawn inward through tubes attached to the bronchii.

The trachea of a Starling, *Sturnus vulgaris*, was cut off close to the syrinx. By inserting a slender blade the semilunar membrane was entirely removed. After this, air was passed through the syrinx as before, and sounds were produced as usual. There was no noticeable modification of sound quality after the removal of the membrane.

From these experiments it seems: 1) that sound is produced, at least in the forms examined, during the active, or exhalant, phase of respiration; 2) that the semilunar membrane has no important function, if any, in the production of sound; and 3) that sound originates in vibrations of the tympaniform membranes set up by air currents from the lungs.

Function of Syringeal Muscles in Production of Sound

Starlings were chosen for this study because they have the full set of seven pairs of syringeal muscles and a wide variety of calls. The syringeal muscle system of Starlings, and of other birds having seven pairs of syringeal muscles (Table 1), is similar to that of the European Raven, *Corvus corax sinuatus*, as described by Owen (1866) and by Shufeldt (1890). Stresemann (1934) gives an accurate, detailed description of the action of the different muscles. The drawings shown in Figures 2 and 3, made from the Eastern Crow, *Corvus brachyrhynchos*, indicate the locations of these muscles.

Since the syrinx lies dorsal to the heart it is difficult to study it in a live, anaesthetized bird. In order to study its structures in living tissues the bird was given ether and dissection begun when it was in the deep breathing state. After the sternum and furculum were removed the heart was found still beating. By quickly removing the heart the syrinx was reached while life remained in the muscles. The electrodes of a 22-volt, dry-cell battery were applied successively to each pair of syringeal muscles. The current contracted the muscles and produced rigor mortis in the contracted state. After each pair of muscles was immobilized air was again passed through the syrinx by drawing it through the trachea with the syringe. Changes in the position of the intermediary bars (Fig. 1) with respect to each other, resultant effects upon the syringeal membranes, and changes in sound were noted.

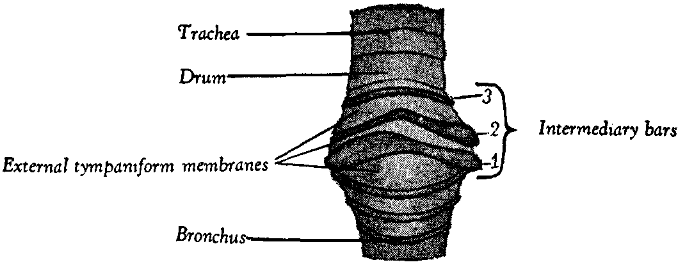

FIGURE 1. Syringeal cartilages of the Crow, right side.

Contraction of *Mm. broncho-trachealis anticus* and *posticus* draws the first intermediary bar cephalad and rotates the cephalad edge of the bar inward. This brings the external and internal tympaniform membranes close together. The current of air through the syrinx then sets up vibrations in the membranes on both sides of the first intermediary bar as well as in the internal tympaniform membrane. During the vibrations the external and internal membranes come in contact, as can be seen through the transparent walls. This action is marked by a noticeable change in tone. A rise in pitch is noted after contraction of *M. broncho-trachealis anticus,* drawing the second intermediary bar cephalad. Contraction of *M. broncho-trachealis brevis* produces an internal fold of membrane cephalad to the third intermediary bar and a slight change in tone. No change in tone can be detected when contraction of *M. bronchialis posticus* draws the second intermediary bar slightly ventral.

These observations, with respect to the changes in tone, are of necessity inaccurate as compared to sounds produced by a living bird, but they give a general idea of the function of the muscles involved.

During these manipulations the bronchidesmus membrane was drawn gradually closer to the intermediary bars. When finally all the muscles were contracted, its edge fitted along the base of the pessulus and the apex of the bronchii, shutting the internal tympani-

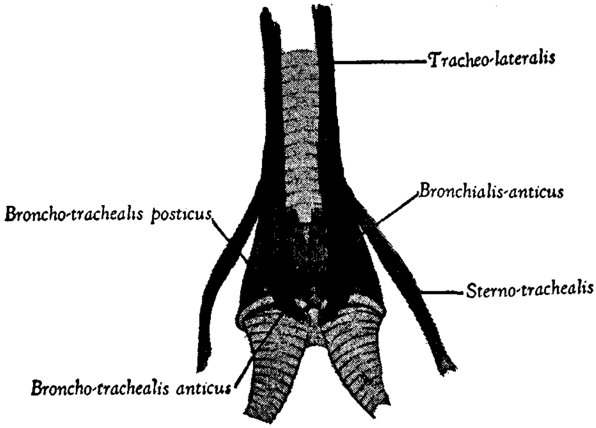

FIGURE 2. Syringeal Muscles of the Crow, ventral view.

form membrane in a tight box between the bronchidesmus membrane and the dorso-syringeal membrane.

Mm. tracheo-lateralis and *sterno-trachealis* work in opposition, the former being the tensor and the latter the releaser of tension of the syringeal membranes. When the trachea and syrinx are in their relaxed positions, sound can be produced artifically only by applying great pressure within the air-sacs. When *Mm. sterno-trachealis* are contracted (or when the trachea is cut) the syrinx moves caudad, the internal tympaniform membrane becomes relaxed and vibrates

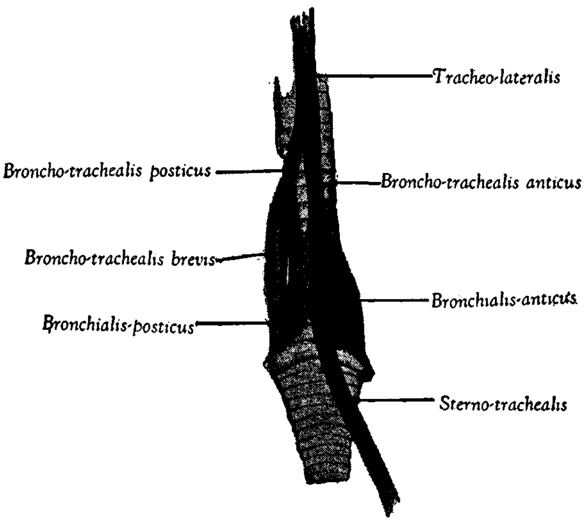

FIGURE 3. Syringeal Muscles of the Crow, right side.

steadily in a current of air directed cephalad. If *Mm. sterno-trachealis* were absent, the membranes would remain taut in a living bird, and presumably no sound would be produced, unless it were by very great pressure within the air-sacs. Four Cardinals, *Richmondena cardinalis*, from which *Mm. sterno-trachealis* were excised were not heard to sing, although control birds kept in the same pens sang freely during the singing season. Two domestic cocks, *Gallus gallus*, on which the same operation was performed succeeded in crowing loudly a few weeks afterward, with unusual contortions of the neck and a somewhat altered tone.

COMPARISON OF THE SYRINGEAL MUSCULATURE OF SOME PASSERINE BIRDS

Detailed studies of the musculature of the syrinx in a number of passerine birds show that not only do many birds lack certain of the seven pairs of syringeal muscles, but that the attachments of the muscles vary widely. The birds I have been able to study are arranged here (Table 1) in five groups according to the number of syringeal muscles possessed by each, and within each group they are arranged according to the attachments of the muscles. Those with attachments allowing the greatest freedom of motion are at the top of the list, and those having only more restricted movement are farther down. A detailed description of one bird in each group is given, which may be considered typical of that group, with deviations indicated in the text. A study of these descriptions will show that while there are exceptions, in general the birds with more muscles and greater freedom of motion produce the wider varieties of sound. This, of course, has no bearing upon the musical qualities of the song as judged by human standards, else one would scarcely rate the Cardinal so far below the Crow.

GROUP A: Catbird, *Dumetella carolinensis;* Crow; Yellow-breasted Chat, *Icteria virens;* House Wren, *Troglodytes aëdon;* Tufted Titmouse, *Parus bicolor.*

Muscles in the Catbird:

1. *Tracheo-lateralis,* on the lateral surface of the trachea.
   Origin: The lateral surface of the thyroid cartilage of the larynx.
   Insertion: It does not insert directly, but bifurcates at the level of the second tracheal ring, giving rise to *Mm. broncho-trachealis anticus* and *posticus.*
   Action: Draws the trachea cephalad.
2. *Broncho-trachealis anticus,* on the ventral surface of the syrinx, external.
   Origin: The bifurcation of *M. tracheo-lateralis.*
   Insertion: The ventral end of the first intermediary bar.
   Action: Draws the first intermediary bar cephalad.

TABLE 1

COMPARISON OF SYRINGEAL MUSCLES PRESENT IN DIFFERENT SPECIES

	Tracheo-lateralis	*Broncho-trachealis anticus*	*Broncho-trachealis posticus*	*Broncho-trachealis brevis*	*Sterno-trachealis*	*Bron-chialis anticus*	*Bron-chialis posticus*	*Total pairs muscles*
GROUP A								
Catbird	x*	x	x	x	x	x	x	7
Starling	x	x	x	x	x	x	x	7
Crow	x	x	x	x	x	x	x	7
Yellow-breasted Chat	x	x	x	x	x	x	x	7
House Wren	x	x	x	x	x	x	x	7
Tufted Titmouse	x	x	x	x	x	x	x	7
GROUP B								
Song Sparrow	x	x	x	x	x	x		6
Horned Lark	x	x	x	x	x	x		6
Cardinal	x	x	x	x	x	x		6
Vesper Sparrow	x	x	x	x	x	x		6
Meadowlark	x	x	x	x	x	x		6
Bobolink	x	x	x	x	x	x		6
Red-eyed Vireo	x	x	x		x	x	x	6
Scarlet Tanager	x	x	x		x	x	x	6
White-breasted Nuthatch	x	x	x		x	x		5
GROUP C								
Cowbird		x	x	x	x	x	x	6
Ruby-crowned Kinglet		x	x	x	x	x		5
Golden-crowned Kinglet		x	x	x	x	x		5
Dickcissel		x	x	x	x	x		5
Goldfinch		x	x	x	x	x		5
Yellow Warbler		x	x	x	x	x		5
Red-wing		x	x	x	x	x		5
Cedar Waxwing		x	x	x	x	x		5
Robin		x	x	x	x	x		5
Bronzed Grackle		x	x	x	x	x		5
GROUP D								
Chipping Sparrow	x	x	x		x	x		5
Barn Swallow	x	x	x		x	x		5
Grasshopper Sparrow	x	x	x		x			4
English Sparrow		x	x		x	x		4
GROUP E								
Alder Flycatcher		?			x	?		3
Wood Pewee		?			x	?		3

* x in this space indicates the presence of the muscle, a blank indicates its absence, and ? indicates doubt as to homology.

3. *Broncho-trachealis posticus*, on the dorsal surface of the syrinx, external.
   Origin: The bifurcation of *M. tracheo-lateralis.*
   Insertion: The dorsal end of the first intermediary bar, by a tendon over the end of the second intermediary bar.
   Action: Draws the first intermediary bar cephalad.
4. *Broncho-trachealis brevis*, on the dorsal surface of the syrinx, internal.
   Origin: The dorsal surface of the first tracheal ring.
   Insertion: The dorsal end of the second intermediary bar.
   Action: Draws the second intermediary bar cephalad.
5. *Sterno-trachealis*, extending ventro-laterally from the syrinx.
   Origin: The lateral cranial process of the sternum.

Insertion: The lateral surface of the first tracheal ring.
Action: Draws the trachea caudad.

6. *Bronchialis anticus,* on the ventral surface of the syrinx, internal.
   Origin: The ventral surface of the first tracheal ring.
   Insertion: The ventral end of the second intermediary bar.
   Action: Draws the second intermediary bar cephalad.
7. *Bronchialis posticus,* on the lateral surface of the syrinx.
   Origin: The latero-ventral surface of the first tracheal ring.
   Insertion: The dorsal end of the second intermediary bar.
   Action: Draws the second intermediary bar ventral.

Each bird of this group possesses seven pairs of syringeal muscles but only in the Catbird, Starling, and Crow do we find the first two intermediary bars with muscle attachments at each end. This arrangement allows the first bar to rotate on its long axis and permits delicate adjustments of tension in the tympaniform membranes. In the Chat the second bar has no dorsal muscle attachments (*Mm. broncho-trachealis posticus* and *brevis* attach to the third bar), and the ventral muscle instead of being at the end of the bar attaches along it for about one-fourth of its length. For this reason the syrinx of the Chat is not quite so mobile as those of the first three birds. There is still less motion in the syrinx of the House Wren; the third intermediary bar has no muscular attachments, and the first and second bars have their ventral muscles attached along half the length of the bars at the cephalad edges. Muscles so attached do not rotate the first intermediary bar on its long axis, nor do they give the delicate precision of adjustments of tension found in the Catbird, Starling, and Crow. In the Titmouse the first intermediary bar has no muscle at the dorsal end, *M. broncho-trachealis posticus* being attached to the third bar instead of the first. The first bar is, therefore, less mobile than that of other birds of this group.

GROUP B: Song Sparrow, *Melospiza melodia;* Prairie Horned Lark, *Eremophila alpestris praticola;* Cardinal; Vesper Sparrow, *Pooecetes gramineus;* Meadowlark, *Sturnella magna;* Bobolink, *Dolichonyx oryzivorus;* Red-eyed Vireo, *Vireo olivaceus;* Scarlet Tanager, *Piranga olivacea;* White-breasted Nuthatch, *Sitta carolinensis.*

Muscles in the Song Sparrow:

1. *Tracheo-lateralis,* on the lateral surface of the trachea.
   Origin: The lateral surface of the thyroid cartilage of the larynx.
   Insertion: It does not insert directly, but bifurcates at the level of the fifth tracheal ring, giving rise to *Mm. broncho-trachealis anticus* and *posticus.*
   Action: Draws the trachea cephalad.
2. *Broncho-trachealis anticus,* on the ventral surface of the syrinx, external.
   Origin: The bifurcation of *M. tracheo-lateralis.*

Insertion: The ventral end of the first intermediary bar.
Action: Draws the first intermediary bar cephalad.

3. *Broncho-trachealis posticus,* on the dorsal surface of the syrinx, external.
Origin: The bifurcation of *M. tracheo-lateralis.*
Insertion: The dorsal end of the first intermediary bar.
Action: Draws the first intermediary bar cephalad.
4. *Broncho-trachealis brevis,* on the dorsal surface of the syrinx, internal.
Origin: The lateral surface of the syringeal drum.
Insertion: The dorsal end of the second intermediary bar.
Action: Draws the second intermediary bar cephalad.
5. *Sterno-trachealis,* extending ventro-laterally from the syrinx.
Origin: The lateral cranial process of the sternum.
Insertion: The cephalad edge of the lateral surface of the syringeal drum.
Action: Draws the trachea caudad.
6. *Bronchialis anticus,* on the ventral surface of the syrinx, internal.
Origin: The ventral cephalad edge of the syringeal drum.
Insertion: The ventral half of the second intermediary bar.
Action: Draws the second intermediary bar cephalad.
7. *Bronchialis posticus,* is not present.

Birds in this group lack either *M. broncho-trachealis brevis* or *M. bronchialis posticus,* or both. In birds having both, we usually find the muscles attached to the ends of the second intermediary bar, giving it motion in two directions, as in the Catbird. In these birds the second bar has but one dorsal muscle attachment, and in some cases it shares that with the third bar, the two being bound together at the dorsal ends. In the Tanager *M. broncho-trachealis posticus* attaches to the dorsal end of the second intermediary bar, leaving the first bar without a dorsal attachment. In the Nuthatch *Mm. broncho-trachealis anticus* and *posticus* attach respectively to the second and third intermediary bars, leaving the first bar without attachment and the second bar with only the ventral muscle.

GROUP C: Cowbird, *Molothrus ater;* Golden-crowned Kinglet, *Regulus satrapa;* Ruby-crowned Kinglet, *R. calendula;* Dickcissel, *Spiza americana;* Goldfinch, *Spinus tristis;* Yellow Warbler, *Dendroica aestiva;* Redwing, *Agelaius phoeniceus;* Cedar Waxwing, *Bombycilla cedrorum;* Robin, *Turdus migratorius;* and Bronzed Grackle, *Quiscalus quiscula.*

Muscles in the Cowbird:

1. *Tracheo-lateralis* is not present.
2. *Broncho-trachealis anticus,* on the ventral surface of the syrinx, external.
Origin: The lateral surface of the sixth tracheal ring.
Insertion: The ventral end of the first intermediary bar.
Action: Draws the first intermediary bar cephalad.
3. *Broncho-trachealis posticus,* on the dorsal surface of the syrinx, external.
Origin: The lateral surface of the sixth tracheal ring.

Insertion: The dorsal end of the first intermediary bar.
Action: Draws the first intermediary bar cephalad.

4. *Broncho-trachealis brevis*, on the dorsal surface of the syrinx, external.
   Origin: The dorsal surface of the fourth tracheal ring.
   Insertion: The dorsal end of the second intermediary bar.
   Action: Draws the second intermediary bar cephalad.
5. *Sterno-trachealis*, extending latero-ventrally from the syrinx.
   Origin: The lateral cranial process of the sternum.
   Insertion: The lateral surface of the first tracheal ring.
   Action: Draws the trachea caudad.
6. *Bronchialis anticus*, on the ventral surface of the syrinx, internal.
   Origin: The ventral cephalad edge of the syringeal drum.
   Insertion: The ventral half of the second intermediary bar.
   Action: Draws the second intermediary bar cephalad.
7. *Bronchialis posticus*, on the lateral surface of the syrinx.
   Origin: The ventral cephalad edge of the syringeal drum.
   Insertion: The dorsal end of the second intermediary bar.
   Action: Draws the second intermediary bar ventral.

These birds lack *M. tracheo-lateralis*, and all but the Cowbird also lack either *M. broncho-trachealis brevis*, *M. bronchialis posticus*, or both. Only the Kinglets, the Dickcissel, and the Goldfinch have the muscles attached to the ends of the intermediary bars; the others have broad attachments of *M. bronchialis anticus* along the second intermediary bar, and the Robin and the Grackle also have broad attachments of *M. broncho-trachealis anticus* along the first bar. This suggests that in this group the Kinglets, the Dickcissel, and the Goldfinch have the more refined muscular control of the intermediary bars and the intervening membranes, while the Robin and the Grackle have the least detailed control and would be expected to have a narrower range of varied notes. The Black and White Warbler, *Mniotilta varia*, and the American Redstart, *Setophaga ruticilla*, have this musculature similar to that in the Yellow Warbler.

GROUP D: Chipping Sparrow, *Spizella passerina;* Barn Swallow, *Hirundo rustica;* Grasshopper Sparrow, *Ammodramus savannarum;* and English Sparrow, *Passer domesticus.*

Muscles in the Chipping Sparrow:

1. *Tracheo-lateralis*, on the lateral surface of the trachea.
   Origin: The lateral surface of the thyroid cartilage of the larynx.
   Insertion: It does not insert directly but bifurcates at the level of the third tracheal ring, giving rise to *Mm. broncho-trachealis anticus* and *posticus.*
   Action: Draws the trachea cephalad.
2. *Broncho-trachealis anticus*, on the ventral surface of the syrinx, external.
   Origin: The bifurcation of *M. tracheo-lateralis.*
   Insertion: The ventral half of the first intermediary bar.
   Action: Draws the first intermediary bar cephalad.

3. *Broncho-trachealis posticus,* on the dorsal surface of the syrinx, external.
   Origin: The bifurcation of *M. tracheo-lateralis.*
   Insertion: The first and second intermediary bars, the two united at their dorsal ends.
   Action: Draws the first and second intermediary bars cephalad.
4. *Broncho-trachealis brevis* is not present.
5. *Sterno-trachealis,* extending ventro-laterally from the syrinx.
   Origin: The lateral cranial process of the sternum.
   Insertion: On *M. tracheo-lateralis,* near the point of its bifurcation.
   Action: Draws the trachea caudad.
6. *Bronchialis anticus,* on the ventral surface of the syrinx, internal.
   Origin: The ventral cephalad edge of the syringeal drum.
   Insertion: The ventral half of the second intermediary bar.
   Action: Draws the second intermediary bar cephalad.
7. *Bronchialis posticus* is not present.

The birds in this group might have been included in Groups B and C, considering the numbers of muscles each possesses, but they are placed separately in order to illustrate the ineffectiveness of muscles whose attachments preclude dexterity of motion in the syrinx. In the Swallow the cartilages are small and very close together. The first intermediary bar is wide and flat, and the expanse of external tympaniform membrane on each side is small. The third intermediary bar has a hammer-like protrusion on the dorsal end which crosses the ends of the other two bars. There is no muscle attachment to the dorsal end of the first intermediary bar. Due to this combination there can be little movement of the cartilages and membranes of the syrinx. The other three birds in the group have very wide attachments of the ventral muscles to the intermediary bars, and in the English Sparrow the dorsal ends of the first two bars are fastened firmly together by a ligament, allowing them no independent motion.

GROUP E: Alder Flycatcher, *Empidonax traillii,* and Eastern Wood Pewee, *Contopus virens.*

In these and other specimens of the Tyrannidae were found syringes differing from both the typical non-passerine syrinx without intrinsic muscles and the syrinx of the Passeres with paired longitudinal muscles. *M. sterno-trachealis* inserts high on the trachea, at about the thirteenth ring, after the manner of the non-passerines, but *M. tracheo-lateralis,* so prominent in non-passerines, is absent. One continuous, broad, flat muscle lies on the ventral surface of the trachea from about the thirteenth ring to the cephalad edge of the drum, and a pair of muscles originating on the mid-ventral line of the drum extends transversely to the dorsal ends of the second intermediary bars. Contractions of these muscles could alter the quality of sound but little.

SUMMARY

Experiments on dissected, anaesthetized birds show that sound is produced by air currents passing through the respiratory tubes in the caudo-cephalad direction and setting up vibrations in the syringeal membranes. Tension on these membranes is regulated primarily by the opposing action of *Mm. sterno-trachealis* and *tracheo-lateralis*, and secondarily by the action of the intrinsic syringeal muscles. Both pitch and quality of sound depend upon the tension control of the syringeal membranes by the intrinsic syringeal muscles.

The arrangement of the birds studied, in the order of the number of syringeal muscles possessed by each species, shows that in general the birds possessing more muscles are able to produce a wider variety of notes than those having fewer muscles, providing that the muscles are attached to the syringeal cartilages in such a way that these cartilages may move freely, regulating with precision the tension on the vibrating syringeal membranes. There is, therefore, direct correlation between the degree of development of the syrinx, with respect to muscles and attachments, and the quality (variety of notes) of the song.

LITERATURE CITED

COLE, ARCH E. 1945. The song-production mechanism of birds. Kentucky Warbler, 21: 17–27.

MILLER, ALDEN H. 1947. The structural basis of the voice of the Flammulated Owl. Auk, 64: 133–135.

OWEN, SIR RICHARD. 1866. The Anatomy of the Vertebrates. (Longman, Green and Co., London), Vol. 2.

PARKER, THOMAS J. AND WILLIAM A. HASWELL. 1940. The Anatomy of the Vertebrates. (Macmillan Co., New York), Vol. 2.

SHUFELDT, ROBERT WILSON. 1890. The Myology of the Raven. (Macmillan Co., New York).

STRESEMANN, ERWIN. 1927–1934. Aves. *In* Handbuch der Zoologie. (Kükenthal). (Walter de Gruyter Co., Berlin), Vol. 7, pt. 2.

THOMSON, ARTHUR. 1923. The Biology of Birds. (Macmillan Co., New York).

Department of Zoology and Entomology, Ohio State University, Columbus, Ohio, August 16, 1950.