only to slight stretching or condensing along the time axis according to what sort of analyzer is being used). If the tones are pure, a violinist can read the spectrogram, because it corresponds to notation on the musical staff, and play the theme on his instrument. Most bird songs, and those of gibbons, are pushed to the upper part of the graph, where "wide band" tracings become narrow enough to give the good pitch resolution of "narrow band" combined with excellent temporal definition characteristic of the "wide band" setting. Moreover the page can be inverted to receive a second tracing on the other half.

For all the above reasons I recommend the acceptance of the log scale in displays of natural sounds for ordinary purposes. The linear scale might be reserved for special studies of harmonics, some of which appear at equal vertical intervals at this setting.

I thank Luis F. Baptista and J. W. Hardy for making the spectrograms and the following persons from the fields of music, mathematics, and physics: James R. Anthony, Robert Exell, Rafael Ronkin, Rolf M. Sinclair, and Carl T. Tomisuka for criticizing this note.—JOE T. MARSHALL, JR., *Fish and Wildlife Laboratories, National Museum of Natural History, Washington, D.C. 20560.* Accepted 7 Aug. 75.

The role of the sternotrachealis muscles in bird song production.—Greenewalt (1968) integrated much of what was known about song production in birds and combined it with acoustical data to produce a predictive model of avian song production. Greenewalt's theory can be separated into two models: 1) "The Passive Closure Model" and 2) "The Active Closure Model" (Gaunt et al. 1973). These models assume that the muscles of the syrinx act to regulate tension on the paired internal tympaniform membrane and possibly to position the paired external labia (see Fig. 1). There is good evidence from physiological studies of the syrinx in dead birds that the syringeal musculature is capable of influencing the tension applied to the internal tympaniform membrane and the external labia (Miskimen 1951; Gross 1964; Chamberlain et al. 1968). With the exception of Gross' (loc. cit.) studies of the Domestic Fowl (*Gallus domesticus*), there have been no attempts to determine the precise function of the syringeal muscles in living vocalizing birds.

This paper reports the results of experiments that attempt to define the role of the sternotrachealis muscles in song production of four species of birds representing two orders and three families of birds.

The four species investigated were: Rock Pigeon (*Columba livia*), Red-winged Blackbird (*Agelaius phoeniceus*), White-throated Sparrow (*Zonotrichia albicollis*), and Song Sparrow (*Melospiza melodia*). Two male individuals each of Red-wings, White-throats, and one Song Sparrow were captured on their

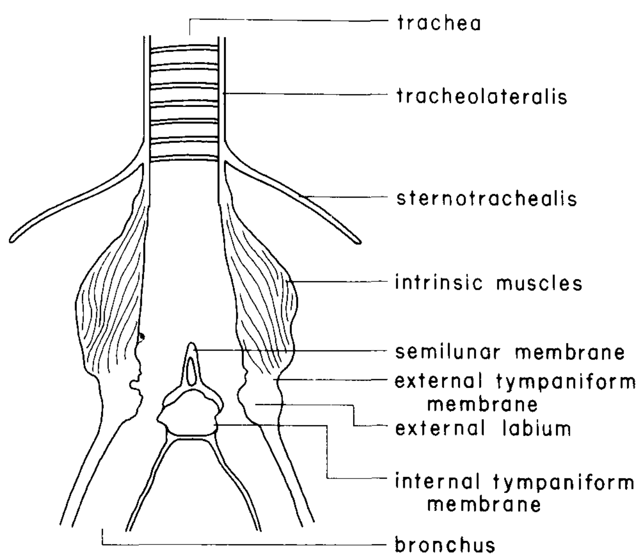

Fig. 1. A schematic representation of structures in the avian syrinx. A longitudinal section of the syrinx exposes the bronchial lumen, external and internal tympaniform membranes, external labia, and location of intrinsic musculature. The tracheolateralis and the sternotrachealis muscles are shown on the outer lateral surfaces of the trachea.

territories and brought into the laboratory. A 5–10 mg pellet of testosterone (Oreton subcutaneous pellets were provided courtesy of Schering Corporation) was implanted in the neck of each and the birds were then placed in individual cages for 10 days. They were subsequently caged within a Tracor sound isolation chamber. To increase the probability of singing by the passerines, species-typical songs were played to each through a tape recorder connected to a speaker mounted inside the chamber. Two pigeons were taken from a local loft, placed in individual cages and given food and water *ad libitum*. Individual birds were caged within a sound isolation chamber. Another pigeon was introduced and this generally induced courtship "song" (cooing) in the first pigeon. Songs of all four species were recorded at 7 ½" per second on a Nagra IV-S tape recorder through a Sennheiser model (#MD 211N) microphone. After good quality recordings were obtained the birds were anesthetized with Equithesin (Jen-Sal Laboratories) or Fluothane (Ayrest). The feathers of the neck were soaked with alcohol and parted along the midline of the neck. Depending on the size of the bird an incision 2–6 cm long was made in the ventral skin of the neck. Access to the membrane bounding the interclavicular air sac was gained by pushing fat and connective tissue aside. The membrane

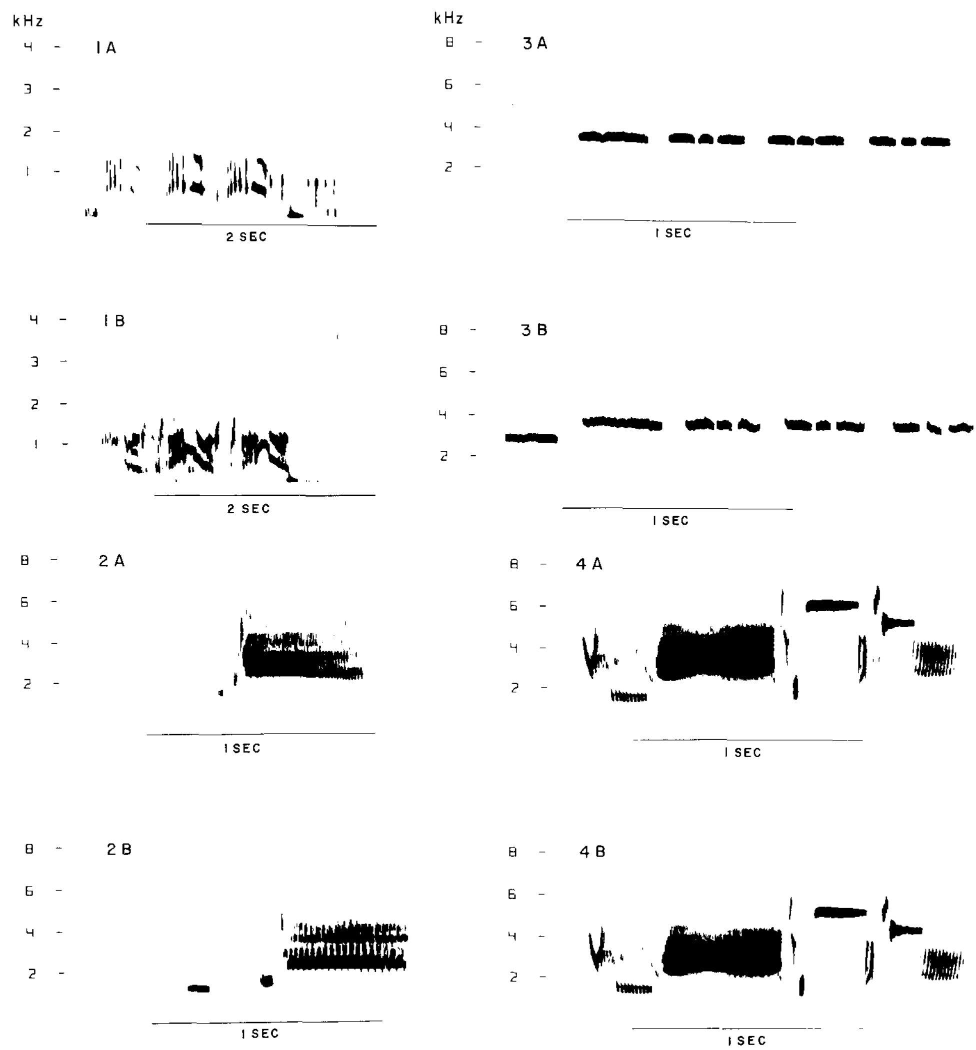

Fig. 2. 1A, preoperative song of the Rock Pigeon; 1B, postoperative song of the same bird; 2A, preoperative song of a Red-wing; 2B, the 14th day postoperative song of the same bird; 3A, the preoperative song of the White-throat; 3B, after the 14th day postoperative song of the same bird; 4A, preoperative song of a Song Sparrow; 4B, the song sung by the same individual after 14th postoperative day.

was then picked up with fine forceps and cut. The syrinx was exposed and the left and right sternotrachealis muscles of each bird were sectioned. The skin (but not the air sac membrane) was closed with interrupted sutures. The birds were allowed to recover for 2 days in an isolation chamber. On the 3rd day species-typical song was played through the loudspeaker to increase the probability of singing in the operated passerines. The birds were so stimulated every day until they sang a normal song. To obtain postoperative recordings from the pigeons, a second pigeon was introduced daily into the isolation chamber housing the operated individual. This was done until the operated pigeon sang a normal song.

After the postoperative recordings were made, all individuals were sacrificed and it was determined that both left and right sternotrachealis muscles had been successfully sectioned in each individual.

Spectrograms of songs were made on a Kay Elemetrics Vibralyzer Model 7030A with a 300 Hz filter and the AGC inactivated.

Aural comparison of the pre- and postoperative song as well as comparison of the spectrograms of the pre- and postoperative song show no significant differences between the songs for any of the birds investigated. Fig. 2 shows an example of the pre- and postoperative song of one bird from each of the four species. The Red-wings, White-throats and Song Sparrows sang a postoperative song between the 4th and 13th postoperative days (see Fig. 3). These bear little resemblance to the postoperative songs these birds sang after the 14th day. The Pigeons sang a normal song on the 9th postoperative day and never produced an atypical song.

The results indicate that the sternotrachealis muscles are not necessary for the production of normal species-typical song in the four species investigated. Although in some cases pre- and postoperative songs

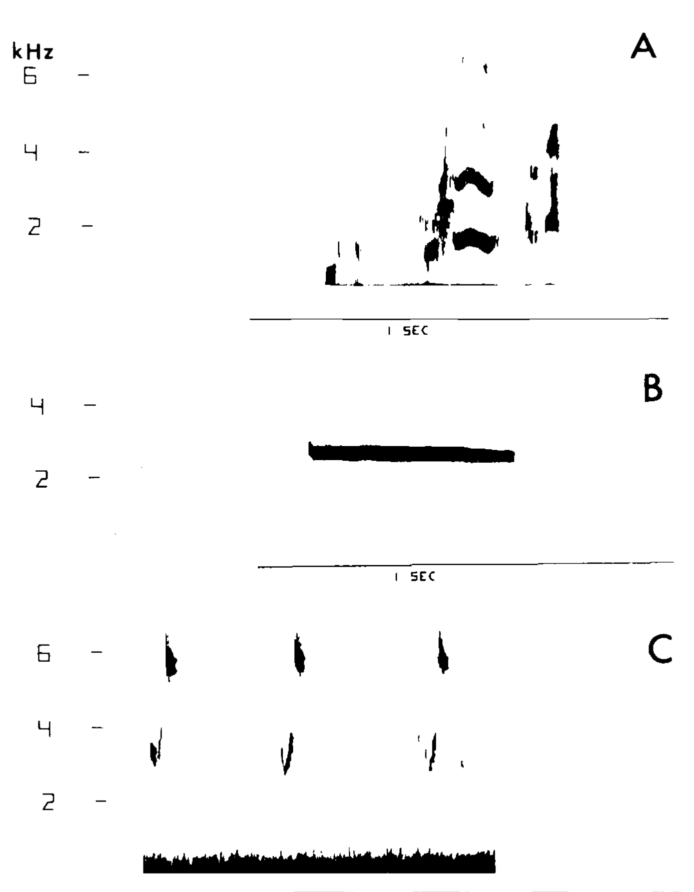

Fig. 3. The songs produced between the 1st and 14th postoperative days for: A, Red-wing; B, White-throat; C, Song Sparrow.

show minor differences, they can be accounted for by the fact that individuals of many species of birds are capable of singing a variety of renditions of the song.

The results reported here are in marked contrast to the conclusions of Miskimen (loc. cit.) who stated that the sternotrachealis muscle along with its presumed antagonist, the tracheolateralis, were primarily responsible for the tension applied to the tympaniform membranes and ultimately the production of song. However, Chamberlain et al. (loc. cit.) conclude that in the Common Crow (*Corvus brachyrhynchos*), the "M. sternotrachealis is a long slender muscle which steadies the syrinx." They attribute no other function to it. Both of these studies were conducted on the syringes of dead birds. Setterwall (1901) also concluded from anatomical considerations that "probably these muscles (sternotrachealis) are too weak to influence the syrinx to any appreciable extent."

It is interesting to note that sectioning the sternotrachealis muscles makes no difference in song production of birds representing two different orders. In addition Gross (1964) found that sectioning the sternotrachealis in the Domestic Fowl did not alter its ability to produce normal vocalizations.

The Red-wings, White-throats, and Song Sparrow, while attempting to sing during the first 14 postoperative days, produced only atypical syllables. I attribute this to the incomplete healing of the air sac membrane. In order to gain access to the syrinx, the interclavicular air sac membrane was opened 2 cm in White-throats and the Song Sparrow, 4–5 cm in the Red-wings, and 5–10 cm in Rock Pigeons. As no attempt was made to close the air sac membrane there was communication between the air sac and other sources of air until healing occurred. Gaunt et al. (loc. cit.) found in Starlings (*Sturnus vulgaris*) that if they opened a cannula placed in the interclavicular air sac, the Starling could not utter normal calls. They stated that "calling was reduced from the normal wail to a feeble "eh . . . eh . . . eh."

The air sacs of the birds investigated in the present study were opened to such an extent that adequate healing of the air sac probably took between 9 and 14 days (unpublished data). After 14 days all birds were able to sing normal species-typical song. From dissections of the sacrificed birds it was determined that the air sac was completely healed at the time of normal song production. An alternative interpretation of these results might be that neural reorganization of some type was necessary for regaining the ability to sing species-typical song and this process took 2 weeks. On other occasions I found that a large incision in the interclavicular air sac alone prevents male Red-wings from singing normal songs for a minimum of 9 days. Cutting the interclavicular air sac membrane constitutes an effective way of temporarily muting birds while producing no apparent impairment of the bird's respiratory processes, which is a problem with the hypoglossal nerve sectioning technique (see Nottebohm 1971 and Smith 1976). This may be of utility for researchers interested in determining the social function of song by temporarily eliminating it in individual birds.

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