SYRINGEAL ANATOMY IN THE COMMON CROW

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A careful study of the functional anatomy of its syrinx in the Common Crow (*Corvus brachyrhynchos*) contradicts the view expressed by Welty (1963) that this species is not capable of vocal versatility, i.e. significant variation in pitch and variety of notes produced.

Poor vocalizers such as most nonpasserines may have only two or three pairs of syringeal muscles, but true song birds typically have seven pairs, and as many as nine pairs have been reported in some song birds (Welty, 1963: 118–119). Owen (1866) and Ames (1965) describe the anatomy of syringeal muscles in the suborder Passeres. Shufeldt (1890) discusses the muscles of the air passages in the raven (*Corvus corax sinuatus*). In a preliminary study of sound production in the Common Crow, Miskimen (1951) reports seven pairs of syringeal muscles. Myers (1917) and Gross (1964) describe the functional anatomy of the chicken (*Gallus domesticus*) syrinx. Ruppell (1933) investigated the vocal structures of the Herring Gull (*Larus argentatus*). His apparatus for holding the syrinx made it possible to observe the vibration of the vocal membranes, but his review of the literature and experimental work all emphasized the importance of pressure in the interclavicular air sac during sound production. Miller (1934) was able to produce sound with the syrinx of the Great Horned Owl (*Bubo virginianus*) and Turkey (*Meleagris gallopavo*) by blowing

Figure 1. Ventral photograph of the syrinx.

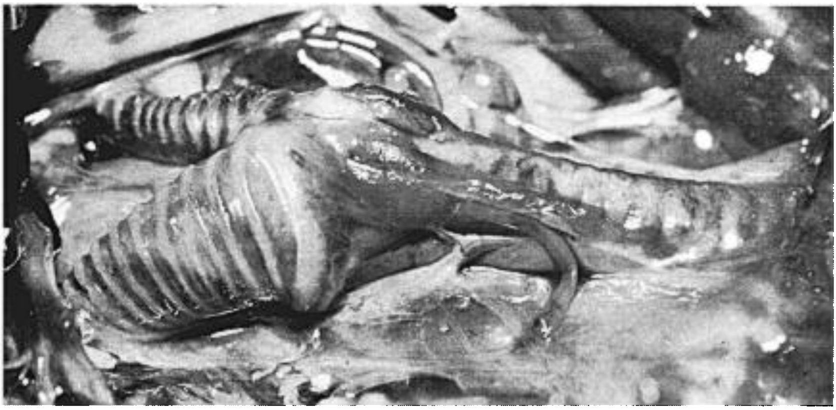

Figure 2. Lateral photograph of the syrinx.

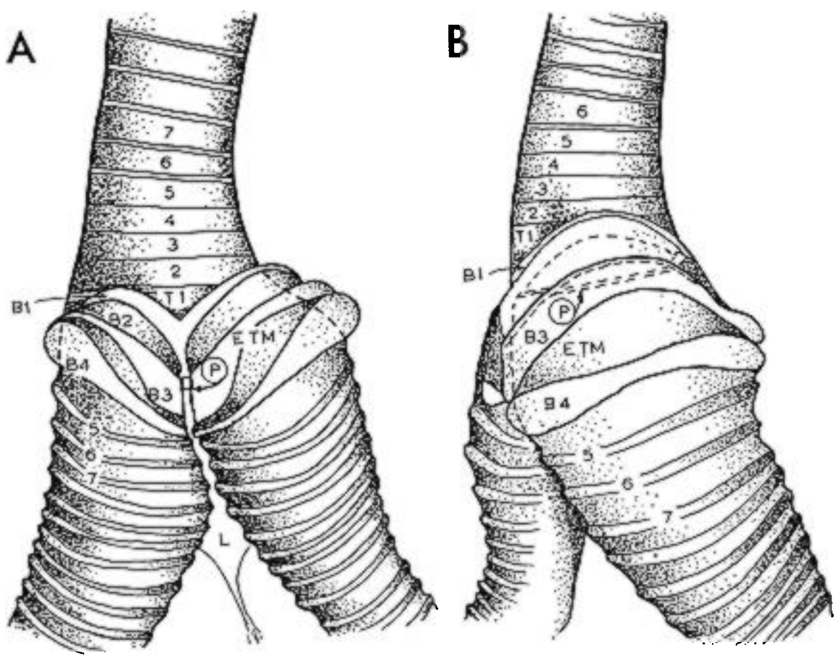

Figure 3. Diagram of bones and cartilages in the syringeal area, A. ventral view, B. lateral view. Key: T1–T7, tracheal rings (bone); B1–B24, bronchial bones; B5–B7, bronchial rings (cartilage); P, pessulus bone; ETM, external tympaniform membrane; L, interbronchial ligament.

TABLE 1
SYRINGEAL MUSCLES IN THE COMMON CROW

Muscle[1]	*Origin*	*Insertion*	*Probable function*
bronchialis anticus, medialis	T[2] 1 2 3[3]	B3 Anterior side at lateral end	Tenses e.t.m.[4]
bronchialis anticus	T 13 14 15	B3 Posterior lateral side of ventral end	Draws posterior margin of B3 outward and forward. B3 has a large ventromedial cartilage which turns the i.t.m.[5] close to the e.t.m.
bronchialis anticus lateralis	T 6	B4 Ventral lateral end and to auxiliary membrane	Relaxes e.t.m. and pulls it away from i.t.m.
bronchialis posticus	T 1 2	B4 Posterior middle to posterior ventral edge and adjacent auxiliary membrane	Tenses e.t.m. dorsally
bronchotrachealis posticus	T 12 13 14 15	B3 Posterior dorsal margin, and by a ligament to dorsal end of B4	Turns anterior margin of B4 medially up to 80° on its longitudinal axis to push e.t.m. medially
sternotrachealis	Sternum 1 cm posterior to clavicle	T 6 and T 7	Steadies syrinx
auxiliary membrane[6]	B3[7] Posterior lateral margin	B4 Posterior lateral margin	Steadies e.t.m. Helps to adjust pitch uniformly

[1] In order; ventral to dorsal aspect.

[2] Tracheal ring.

[3] T rings 1–5 are from tympanum; T rings 6– are from trachea.

[4] External tympaniform membrane.

[5] Internal tympaniform membrane.

[6] Membrane is not muscle; is exterior to e.t.m.

[7] Bronchial ring.

compressed air through the bronchi without added pressure around the syrinx.

Stresemann (1934) asserts that in passerine birds the vibrations caused by air passing over the tympaniform membrane produces the sounds heard

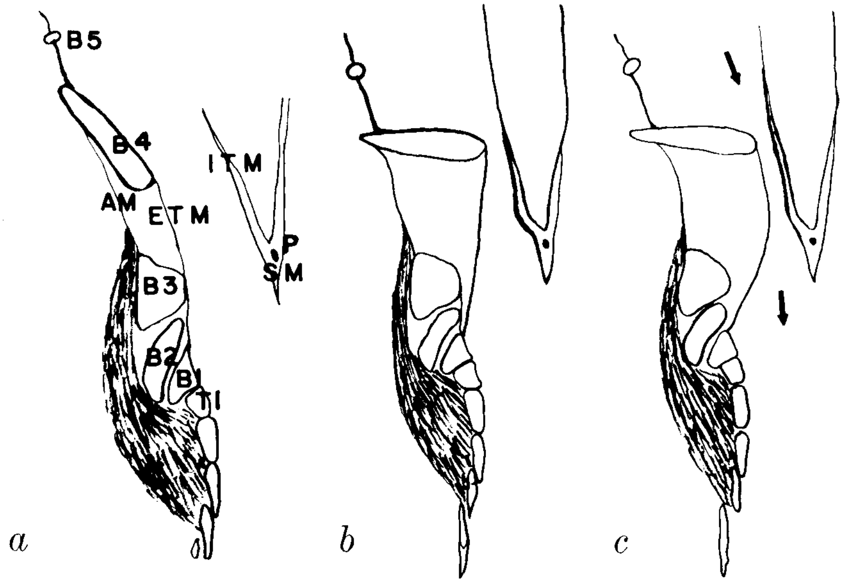

Figure 4. Transverse diagram of the syrinx showing three stages of sound production. A. Syrinx during normal breathing. Sound cannot be produced. B. Syrinx ready for sound production. The rotation of B4 brings the external tympaniform membrane closer to the internal tympaniform membrane. The rotation of B3 by *M. bronchialis anticus* brings the anterior portion of the internal tympaniform membrane closer to the external tympaniform membrane. C. Rapid passage of air brings the membranes close together (Bernoulli effect) and causes the membranes to vibrate, thereby producing sound in the column of air.

Key: T1, tracheal ring (bone); B1–B4, bronchial bones; B5, bronchial ring 5 (cartilage); P, pessulus bone; ETM, external tympaniform membrane; ITM, internal tympaniform membrane; AM, auxiliary membrane; arrows, direction of air.

in song, and that in song birds the intrinsic syringeal muscles regulate the tensions of these membranes.

The objectives of the research reported here were to: (1) determine the way in which sound is produced in the Common Crow and, (2) explain the anatomy and probable function of the syringeal components in this species.

Methods

For this investigation 55 Common Crows were collected for syringeal examination during the winter of 1964 and fall of 1966. All were shot within 25 miles of Blacksburg, Virginia. Fresh syringes were dissected and examined *in situ* under a 15-power binocular microscope. Those used for microscopic examination were preserved in a 10 per cent formalin and normal saline solution in the field. Syringeal tissue was processed by the standard paraffin method in an automatic tissue processing device, sectioned, mounted on slides, and stained with hematoxylineosin and Verhoeff's iodine

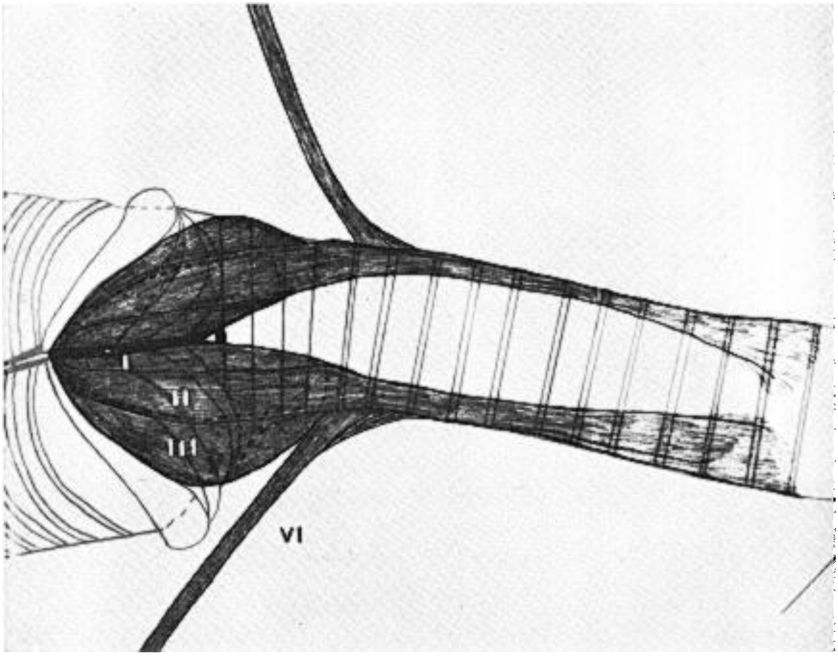

Figure 5. Ventral diagram of the muscles in the syrinx. Key: I, *M. bronchialis anticus medialis*; II, *M. bronchialis anticus*; III, *M. bronchialis anticus lateralis*; VI, *M. sternotrachealis.*

iron hematoxylin, a selective stain for elastic tissue. Numerous attempts were made to produce micro slides that would show the relationship between the parts of the syrinx. All methods that we used resulted in considerable distortion particularly of the external tympaniform membrane (e.t.m.) and auxiliary membranes.

Proposed functions of the muscles (following the muscle nomenclature of Ames (1965)) were based on a careful determination of origin and insertion, and by manipulating the muscle while attempting to produce sound (Table 1). Sound can be produced in birds by inserting a tube into the trachea. The connection between the tube and windpipe must be tight and the posterior air sacs must be open. Sucking on the tube causes the external tympaniform membranes to vibrate, thereby producing sound. The vibrating membranes are clearly observable. This system eleminates the need for a pressure chamber as the pressures around the syrinx and in the bronchi are equal and greater than that of the trachea.

RESULTS AND DISCUSSION

The Common Crow syrinx is bronchotracheal (Figures 1 and 2). In this type the last three to six rings at the base of the trachea enlarge to form the tympanum, posterior to which are added the enlarged first three crescent-shaped rings of each bronchus.

All the tracheal rings in the area of the syrinx, as well as the first four bronchial rings, are ossified and contain hematopoietic bone marrow. The

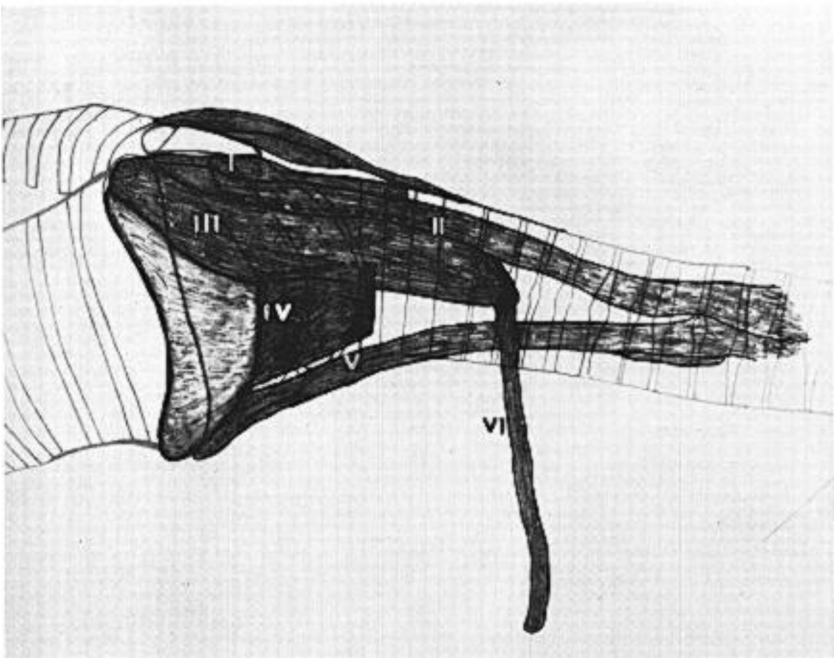

Figure 6. Lateral diagram of the muscles in the syrinx. Key: I, *M. bronchialis anticus medialis*; II, *M. bronchialis anticus*; III, *M. bronchialis anticus lateralis*; IV, *M. bronchialis posticus*; V, *M. bronchotrachealis posticus*; VI, *M. sternotrachealis.*

tympanum, composed of fused masses of the first four tracheal rings and first bronchial ring, serves as a firm anterior support for the syrinx. Anteriorly the trachea is composed of rings which slide over each other allowing considerable anterior–posterior flexibility. Posteriorly the second and third bronchial rings are slightly movable so that the syrinx can be shortened for the adjustment of pitch and still remain rigid (Figure 3).

The e.t.m. is attached anteriorly to the posterior edge of the first bronchial half ring and posteriorly to the middle of the fourth bronchial ring (Figure 3). Most of the membrane is lined with a thin layer of stratified squamous epithelium instead of columnar ciliated cells, which are present in the tracheal–bronchial region (Figure 3) where they line the extreme dorsal and ventral portions of the bronchi in the vocal area.

The internal tympaniform membrane (i.t.m.) extends posteriorly from the semilunar membrane to the bronchial wall (Figure 4C). Midway between the dorsal and ventral margins, opposite the e.t.m., a fibrous bar extending posteriorly from the semilunar membrane and pessulus (Figures 3 and 7B) tends to stiffen the membrane.

M. bronchotrachealis posticus is attached to the ventral end of B3 via

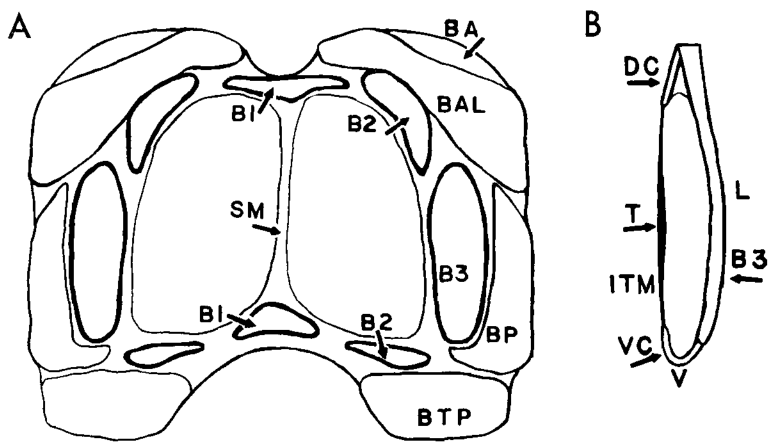

Figure 7. Frontal diagrams of A. syrinx and B. third bronchial ring. Key: BA, *M. bronchialis anticus*; BAL, *M. bronchialis anticus lateralis*; BP, *M. bronchialis posticus*; B1–B3, bronchial bones; SM, semilunar membrane; V, ventral; L, lateral; DC, dorsal cartilage; ITM, internal tympaniform membrane; T, thickened area in ITM; VC, ventral cartilage.

a ligament. The ventral end of bronchial ring 3 (B3) is connected to the ventral end of bronchial ring 4 (B4) by a ligament that rotates B4 up to 80° when B3 is pulled approximately 1 mm anteriorly (Figure 8). This action brings the e.t.m. closer to the i.t.m., thus adjusting the tension of the e.t.m. which alters the pitch of the sound (Figure 4). *M. bronchialis anticus medialis* and *M. bronchialis posticus* draw B3 toward the tympanum (Figures 5 and 6). B3 is attached to and pulls the auxiliary membrane which is also attached to B4. This action turns B4 inward which results in increased tension on the e.t.m., and also brings it closer to the i.t.m. Tension on the auxiliary membrane steadies B4 during sound production. The small closed space between the auxiliary membrane and the e.t.m. can be demonstrated by injecting fluid between the two membranes.

M. bronchotrachealis posticus relaxes and pulls the e.t.m. away from the i.t.m. by reversing the rotation action of *M. bronchotrachealis posticus* and by pulling the anterior ventral margin of B4 outward. In this way, it functions as a "spoiler" muscle—allowing an abrupt cut-off of sound. *M. bronchialis anticus* draws the posterior margin of B3 outward and forward, thereby rotating the i.t.m. closer to the e.t.m. (Figure 4). *M. sternotrachealis* is a long, slender muscle which steadies the syrinx (Figure 6).

When the syrinx is at rest, the e.t.m. (vocal membrane) is not close to the i.t.m. and no sound can be produced. The intrinsic muscles bring the e.t.m. and i.t.m. closer together under variable tension. Air passing

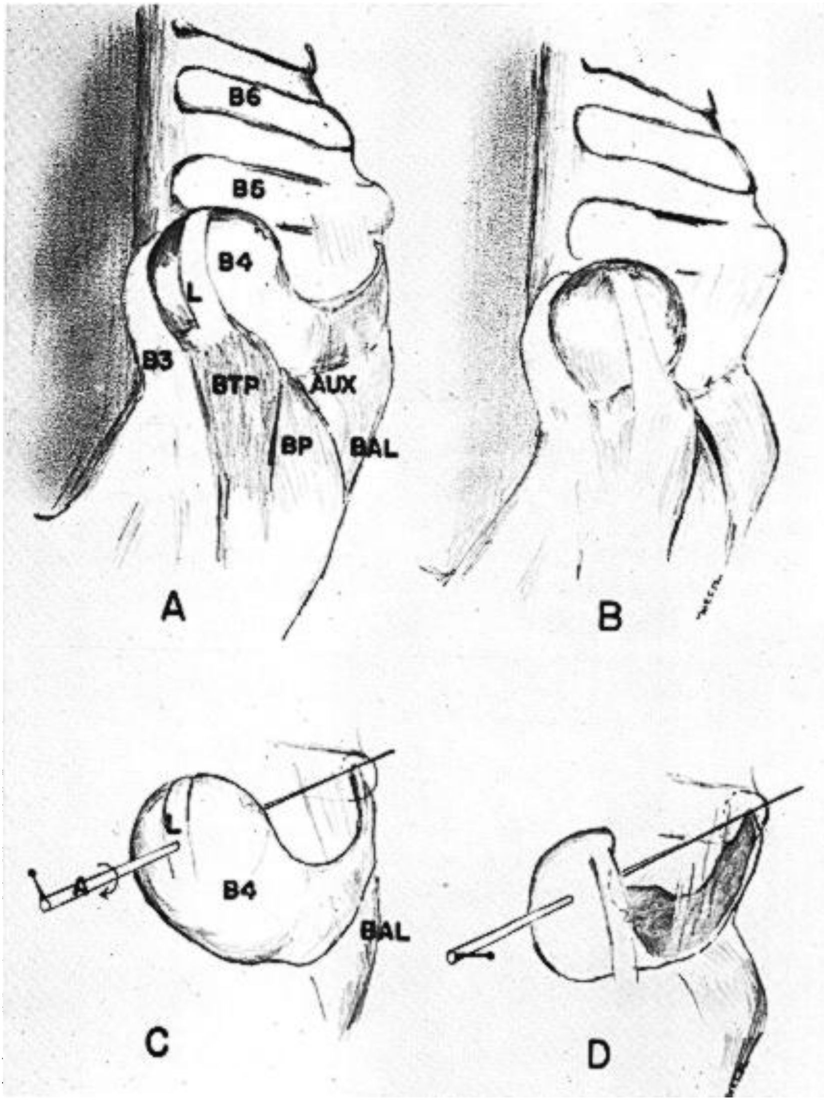

Figure 8. Diagram of the rotation of B4 from the dorsal aspect of the left side of the syrinx. A. Normal position. B. Slight anterior movement of B3 pulls L laterally which rotates the anterior margin of B4 inward. C. Normal position of B4 and L illustrating axis of rotation. D. Maximum rotation of B4 by L.

Key: B3–B6, bronchial rings; BTP, *M. bronchotrachealis posticus*; BAL, *M. bronchialis anticus lateralis*; L, ligament between dorsal ends of B3 and B4.

rapidly caudocephalically between the e.t.m. and i.t.m. tends to draw these membranes closer together during exhalation (Bernoulli effect) thereby causing the e.t.m. to vibrate, producing sound in the column of moving air (Figure 4). Lengthening the e.t.m. increases the pitch by increasing tension. Pressure must be nearly equal in the bronchi and interclavicular air sac before sound can be produced (Ruppell, 1933; Gross, 1964).

ACKNOWLEDGMENTS

Release 66-2 of the Virginia Cooperative Wildlife Research Unit, Virginia Commission of Game and Inland Fisheries, Virginia Polytechnic Institute, Wildlife Management Institute, and U. S. Fish and Wildlife Service, cooperating. This investigation was financed by the Frank M. Chapman Memorial Fund and the Virginia Commission of Game and Inland Fisheries. The authors wish to thank W. E. C. Moore, Department of Veterinary Science, for drawing Figure 8.

SUMMARY

Careful dissections of 55 Common Crows collected in the field revealed that four pairs of bronchial rings, five tracheal rings, one pair of external tympaniform membranes, one pair of internal tympaniform membranes, one pair of auxiliary membranes, and six pairs of muscles are the components of sound production in the syrinx. They function by adjusting the distance between the external and internal tympaniform membranes and by adjusting the tension on the external tympaniform membrane.

Experiments on dissected crow syringes show that sound is produced by air currents passing anteriorly through the respiratory tubes, thereby eliciting vibrations in the external tympaniform membranes.

LITERATURE CITED

AMES, P. L. 1965. The morphology of the syrinx in passerine birds: its application to the classification of the order passeriformes. Ph.D. thesis, New Haven, Connecticut, Yale Univ.

GROSS, W. B. 1964. Voice production by the chicken. Poultry Sci., **43:** 1005–1008.

MILLER, A. H. 1934. Vocal apparatus of some North American owls. Condor, **36:** 204–213.

MISKIMEN, M. 1951. Sound production in passerine birds. Auk, **68:** 493–504.

MYERS, J. A. 1917. Studies on the syrinx of *Gallus domesticus.* J. Morphol., **29:** 165–214.

OWEN, R. 1866. Anatomy of vertebrates, vol. 2. London, Longmans Green.

RUPPELL, W. 1933. Physiologic and Apustik der Vogelstimme. J. f. Orn., **81:** 433–542.

SHUFELDT, R. W. 1890. The myology of the raven. London, MacMillan Co.

STRESEMANN, E. 1934. Aves. *In* W. Kükenthal [ed.]. Handbuch der Zoologie, vol. 7, pt. 2. Berlin, Walter der Gruyter Co.

WELTY, J. C. 1963. The life of birds. New York, Alfred A. Knopf.

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