THE STRUCTURE OF THE CLOACAL PROTUBERANCE OF THE VESPER SPARROW (*POOECETES GRAMINEUS*) AND CERTAIN OTHER PASSERINE BIRDS

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WHEN collecting passerine birds it has long been my custom to sex them in the field by an external examination of the cloacal region. In males this region swells considerably prior to the breeding season to form a definite protuberance. The organ persists throughout the breeding season after which it regresses and disappears. Its use as a diagnostic characteristic for sex is therefore confined to the breeding season, but at that time it is particularly useful in sexing those sparrows in which there is no sexual dimorphism. The fact that ornithologists of my acquaintance were not familiar with this organ, and the lack of reference to it in most treatises and papers on the avian reproductive system, suggested a study of its structure as a preliminary to further investigation.

HISTORICAL REVIEW

Fatio (1864) noted the protuberance on Accentor albinus [=Prunellacollaris]. Gadow and Selenka (1891: 837) state that it reaches its highest state of development in the Alpine Accentor and in the African genus Textor. Stresemann (1934) mentions the protuberance on the American Robin (Turdus migratorius) and on the Red-eved Towhee (Pipilo ervthrophthalmus). Rowan (1929) failed to notice it on the Slate-colored Junco (Junco hyemalis). No mention of a protuberance on the English Sparrow (Passer domesticus) is made by Keck (1934), Riley (1937, 1938), Witschi (1936, 1945), or Witschi and Woods (1936). Witschi (personal communication), however, says that he noticed it but considered it an edematous condition. The sex organs of the Starling (Sturnus vulgaris) have been the subject of investigations by Bullough (1942), Bissonnette (1930a, b, 1931, 1936) and Witschi (op. cit.). Bullough's work in particular treats in great detail all parts of the reproductive system of both male and female; but, in common with the other writers, he says nothing of a protuberance of the cloacal region of the breeding male. Drost (1938) found the protuberance on the English Sparrow, the Starling, and several other species of European passerine birds. Blanchard (1941) and Blanchard and Erickson (1949), in their works on the White-crowned Sparrow (Zonotrichia leucophrys) also failed to mention this region. In the present studies a cloacal protuberance has been observed on breeding males of the Slate-colored Junco, the English Sparrow, the White-crowned Sparrow, and other passerines.

MATERIALS AND METHODS

Specimens were collected with fine shot and were examined immediately in the field and later in the laboratory. Parts required for microscopic study were removed in the field and fixed in Bouin's fluid. Serial sections of cloacal protuberances were cut at 20 microns, and from one set a wax-plate model was made by using camera lucida templates. Other sections were cut at various thicknesses and stained with Delafield's haematoxylin and eosin, Mallory's connective tissue stain, or Weigert's elastic tissue stain. Freshly-killed specimens were dissected in the laboratory, and drawings were made from such dissections.

Although the primary subject of this investigation was the Vesper Sparrow, parallel studies were made on the Horned Lark (Eremophila albestris) and the Chestnut-collared Longspur (Calcarius ornatus). The Clay-colored Sparrow (Spizella pallida), Brewer's Blackbird (Euphagus cyanocephalus), the Purple Grackle (Ouiscalus quiscula), and the Black and White Warbler (Mniotilta varia) were studied less intensively. Since starting this investigation, I have collected no passerine species on which some indication of a cloacal protuberance was lacking on the breeding male. Conversely, no non-passerine species has been collected on which a cloacal protuberance was evident (figure 3). In addition to the above-mentioned passerines, I have observed the cloacal protuberance on the following species: Robin (Turdus migratorius), Yellow-throat (Geothlypis trichas), House Sparrow (Passer domesticus), Western Meadowlark (Sturnella neglecta), Vellow-headed Blackbird (Xanthocephalus xanthocephalus), Redwing (Agelaius phoeniceus), Cowbird (Molothrus ater), Spotted Towhee (Pipilo maculatus), Savannah Sparrow (Passerculus sandwichensis), Leconte's Sparrow (Passerherbulus caudacutus), Sharp-tailed Sparrow (Ammospiza caudacuta), Slate-colored Junco (Junco hyemalis), Whitecrowned Sparrow (Zonotrichia leucophrys), and McCown's Longspur (Rhynchophanes mccowni).

STRUCTURE OF PROTUBERANCE

In form, the cloacal protuberance appears as a spherical appendage on the Vesper Sparrow, the Clay-colored Sparrow, and the Sharptailed Sparrow (figure 2). On the Horned Lark, it has a cylindrical or truncated-conical form (figure 4). Present data are insufficient to show whether the shape of the protuberance is similar within taxonomically defined groups other than species. Changes in size and shape naturally occur during development and regression of the in-

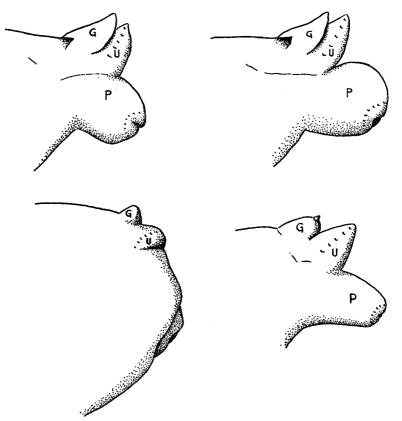


FIGURE 1. Upper left. Cloacal protuberance of male Vesper Sparrow, not fully developed. (Specimen 121, Calgary, Alberta, May 14, 1947.) \times 2.

FIGURE 2. Upper right. Fully developed cloacal protuberance of male Vesper Sparrow. (Specimen 129, Calgary, Alberta, June 1, 1947.) \times 2.

FIGURE 3. Lower left. Cloacal region of male Pectoral Sandpiper (Erolia melanotos) showing no evidence of protuberance. (Specimen 124, Calgary, Alberta, May 17, 1947.) $\times 2$.

FIGURE 4. Lower right. Fully developed cloacal protuberance of male Horned Lark. (Specimen 135, Calgary, Alberta, June 21, 1947.) \times 2. (G—Preen gland; U—Uropygium; P—Cloacal protuberance.)

dividual organ, but variations in the fully-developed protuberance within a species are minute.

In male Vesper Sparrows during the breeding season, the region immediately surrounding the cloaca protrudes postero-ventrally carrying the anus several millimeters from its original position. A roughly spherical body, slightly flattened on its ventral surface, is thus formed (figures 1 and 2). Its greatest diameter is about 10 mm. On the

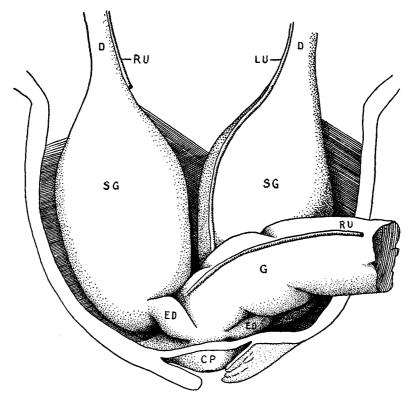


FIGURE 5. Ventral dissection of fully developed cloacal protuberance of male Vesper Sparrow. Gut displaced to left, fat and connective tissue removed to show major organs. \times 8. (C.P.—Cloacal papilla; D.—Ductus deferens; R.U., L.U.—Right and left ureters; S.G.—Seminal glomus; G.—Gut; E.D.—Ejaculatory duct.)

distal surface is the anal opening encircled by thickened lips. The lips are often open, exposing the anterior wall of the proctodaeum which forms a smooth papilla on whose surface is the aperture of the urodeum (figure 2).

Upon dissection the protuberance is found to contain the ends of the digestive tract, the genital ducts, and the ureters (figure 5). Connective tissue and fat fill the interstices. The digestive tube occupies a median ventral position. Along its dorsolateral surfaces run the ureters. Extending dorsally and laterally over the digestive tube and filling the remainder of the protuberance are two large pearshaped bodies formed of the coiled ends of the gonaducts. Though they are in contact in a median line, they remain distinct within their separate sheaths of connective tissue. To their proximal ends the deferent ducts lead and from their distal surfaces come a pair of large

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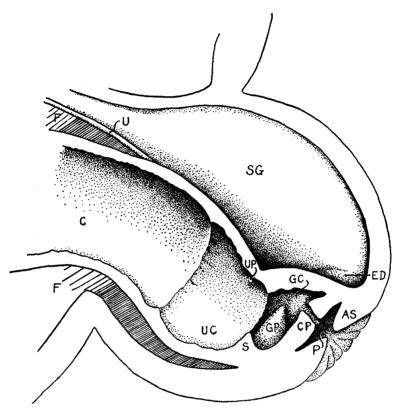


FIGURE 6. Right half of fully developed cloacal protuberance of Vesper Sparrow. \times 8. (A.S.—Anal sphincter; C.—Coprodeum; C.P.—Cloacal papilla; E.D.—Ejaculatory duct; F.—Connective tissue and fat; G.C.—Genital chamber of urodeum; G.P.—Genital papilla; P.—Proctodeum; S.—Sphincter separating urinary and genital chambers; S.G.—Seminal glomus; U.—Ureter; U.C.—Urinary chamber of urodeum; U.P.—Urinary papilla.)

muscular ejaculatory ducts which pass ventrally around the cloaca to enter it from the ventral surface.

The coprodeum, the anterior cloacal chamber, contains no elements of the reproductive system. The urodeum is divided by low folds of its walls into two chambers. The anterior, urinary chamber (figure 6, U.C.) is a short compartment on whose roof the ureters open on two minute papillae. The mucosa of this chamber is thrown into low irregular folds and contains short tubular glands. The lamina propria is rich in lymphoid tissue, small nodules being quite numerous. The submucosa and tunica muscularis are thin. A short distance posterior to the openings of the ureters, the tunica muscularis is strengthened by a strong sphincter muscle which causes the wall to protrude into the cavity (figure 6, S). This sphincter separates the urinary chamber of the urodeum from the succeeding genital chamber.

The genital chamber of the urodeum (figure 6, GC) is a short, irregular chamber extending back to the sphincter of the cloacal papilla over which its cavity extends dorsally and laterally. No evidence of a vestigial bursa of Fabricius has been observed in adult males. From the floor of the chamber two long conical papillae (figure 6, GP) They arise close together on each side of a project into its cavity. median line and reach dorsally toward the cloacal opening. On their tips open the ejaculatory ducts. With the closing of the sphincter immediately anterior to them they are forced back close to the urodeal opening through the cloacal papilla so that the ejaculate may be emitted through the urodeal opening with a minimum of obstruction. About midway in this chamber on a line running up the genital papillae to their tips the epithelium changes abruptly from a columnar to a stratified type, the anterior half of the genital chamber and papillae thus being covered with simple columnar glandular epithelium while the posterior half is covered with stratified epithelium. This latter type of epithelium extends back through the urodeal aperture into the proctodeum.

The proctodeum (figure 6, P) extends posteriorly from the muscular cloacal papilla to the anal opening. Its walls, including the cloacal papilla, are supplied with striated muscle and voluntary control may be assumed. The mucosa is of stratified epithelium on whose surface short simple tubular glands open. As elsewhere throughout the cloaca, lymphoid tissue, scattered or in discrete nodules, is present in the lamina propria and submucosa. During coition the proctodeum may be partially everted, the cloacal papilla being carried through the anal opening. The lips surrounding the anal opening are drawn back to facilitate this process.

During May and June the seminal glomera are the largest and most obvious organs in the cloacal protuberance of the Vesper Sparrow. They are slightly flattened, pear-shaped bodies about 8 mm. long, 4 mm. wide and 4 mm. deep. According to Bullough (1942) these organs in the Starling consist of the much-coiled posterior ends of the vasa deferentia together with a number of blind pouches of the vasa. He calls the organs seminal vesicles. He attributes their increase in size during the spring not only to a lengthening and widening of the gonaducts but also to an increase in number and size of these blind pouches. Witschi (1945) on the other hand, working with the same species, finds no branches of the gonaducts and calls their coiled ends

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glomera. During the present work ten of these organs from the Vesper Sparrow were teased apart and each proved to be a continuous duct with no diverticulae or pouches. Serial sections of others were examined and in no instance could a branching of the duct be found. This was also true for similar organs taken from the Horned Lark, the Chestnut-collared Longspur, and Brewer's Blackbird. In each case, the end of the vas was an unbranched, much-coiled body which may best be termed a seminal glomus. Fatio (1864) says that in the Alpine Accentor, the uncoiled duct would be at least one meter long. In the Vesper Sparrow, it is estimated to be about 80 cm. long.

In the Vesper Sparrow the lumen of the glomeral duct when filled with spermatozoa varies from 150 to 315 microns in diameter, the average being about 250 microns. There appears to be no regularity in the variation. It is probably caused by temporary congestion of semen in certain parts of the duct. The lining epithelium is of a low columnar type. Referring to that of the Starling, Bullough (1942) says that these cells "were seen to be ciliated and very actively secreting." In the Vesper Sparrow, the epithelium shows ample evidence of secretion of an apocrine type, the inner surfaces of the cells being drawn out into beads as their ends are pinched off in the secretory process. No cilia, however, were noticed. The tunica of the duct contains both connective tissue and smooth muscle. In the proximal coils, these tissues are intermingled, but farther down the duct a thin inner sheath of connective tissue and an outer muscular sheath become distinct. The connective tissue contains collagen fibers and a small amount of elastic fiber. The interstices between the coils of the glomeral duct contain loose connective tissue in which run many small blood vessels and capillaries.

At the distal end of each glomus, the duct becomes more muscular and more regularly circular in section as it gradually forms the ejaculatory duct. The lumen becomes reduced as the walls thicken. The ejaculatory duct becomes distinct from the glomus at its distal end and makes a single forward loop as it travels a distance of about three millimeters to the ventral wall of the cloaca, the entrance to which has been previously described. The lining epithelium of columnar cells is thrown into longitudinal ridges indicating that the duct is Its tunica is very thick and consists mainly of smooth distensible. muscle with a small amount of connective tissue. No elastic fiber is present. The papillae on which these ejaculatory ducts open in the genital chamber of the cloaca are merely free extensions of the duct. They are approximately 1.2 mm. in length and 0.5 mm. in diameter. Two large ganglia lie dorsal to the cloaca near the ends of the ureters.

From visual evidence only, I believe post-ganglionic fibers from these ganglia innervate the glomeral ducts.

REGRESSION OF PROTUBERANCE

Following the breeding season, the protuberance becomes smaller. In specimens taken at the end of August, it had almost disappeared. Owing to the migratory habit of the Vesper Sparrow, no specimens were available after this time, and it is not known whether or not there is further regression during fall and winter months.

Within the protuberance changes occur mainly in the glomeral ducts. These shorten and become thinner causing the glomera to become reduced in size. The ejaculatory ducts and the genital papillae are also greatly reduced. By the middle of July, the walls of the glomeral duct have become apposed in many places and the lumen disappears or is greatly reduced. The epithelium has become cuboidal or occasionally squamous. The connective tissue coat is more fibrous, and the wall of the duct is relatively thicker. The interstitial tissue has also become more dense, and it is difficult to define the duct in some places. By the end of August these changes have progressed until the lumen of the duct has disappeared and the glomus appears as a tightly wound cord firmly embedded in connective tissue.

DISCUSSION

This study indicates that as a result of the growth of those parts of the gonaducts known as the seminal glomera, an external protuberance is produced at the cloacal region of the Vesper Sparrow and certain other passerine birds. This protuberance is largest at the height of the breeding season when the seminal glomera are largest. However, the protuberance is something more than a hernia caused by the enlarging glomera; the whole end of the gut tract accompanies it as it develops. This is possibly caused by the close attachment of the glomera and the ejaculatory ducts to the end of the gut. As the glomera lengthen, the ejaculatory ducts are forced distally and the end of the gut follows them. In this manner, the whole of the cloacal region is pushed out to form the cloacal protuberance.

It is not known that the development of the protuberance is synchronous with that of the testes. Indeed, observations made during this study indicate that the growth of the protuberance may lag behind that of the testes. Witschi (1945) has shown that growth of the gonaducts is dependent upon the production of hormones and spermatozoa by the testes. In the Starling, he finds that the cycle of development of the gonaducts is closely linked with the cyclical development of the testes "with a slight lag at the beginning." If a similar relationship can be assumed for the Vesper Sparrow, a correlation in size of the testes and the cloacal protuberance must exist at all times, and the development of each could be estimated from the size of the other. Thus an external appendage, the cloacal protuberance, would serve as an indicator of sexual development in a male bird.

The measurement of sexual development in living birds without the necessity of mutilation or sacrifice of the experimental animal has long posed a problem to those who work on the avian reproductive cycle. Witschi and Woods (1936) used the bill color of the English Sparrow as an indicator for the male sex hormone, but the difficulty of measuring fine gradations of color limited the value of this feature. The cloacal protuberance undergoes a development whose range may be even greater than that of the testes and which lends itself readily to biometric methods. The necessary work required to show to what extent the cloacal protuberance may be used as an external indicator of testicular development has not yet been completed.

SUMMARY

A protuberance of the cloacal region has been observed during the breeding season on several species of passerine birds.

The cloacal protuberance of the Vesper Sparrow is described and a histological description of its major components is given.

The development of the protuberance is believed to be caused by the development of the seminal glomera.

It is suggested that the cloacal protuberance can be used as an external indicator of sexual development in some passerine birds.

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