

Anatomical specializations for generating or modifying sounds occur in the male vocal tract of many

components (Cannell 1988). was examined in a subset of fresh common eiders only, because this muscle was not preserved in most specimens.

Vocal properties of birds are influenced by tracheal size, so in addition to tracheal length we estimated tracheal volume ( $\pm$

slightly caudal and dorsal to that insertion.

originated on the dorsal fascia of the thorax, ~1 cm behind the furcula (origins on the left and right sides were close to the midline, being separated by ~15 mm in a male common eider). It was closely associated with the membrane of the trachea, whose inner surface was covered by a thin sheet of muscle; the muscle was inserted on the sides of the trachea just caudal to and in close association with the cranial edge of the tracheal ring. The trachea emerged from the furcula around tracheal ring numbers ~15–25 (counting cranially from the syrinx). There were ~25–30 rings in each primary bronchus. Because of ossification, the trachea was not distensible; however, the lower esophagus was highly distensible, to ~55 mm in diameter × 90 mm in craniocaudal length in a female, and ~55 × 95 mm in a male common eider when inflated fully with air.

The trachea was thicker in males than females, and was thicker on the left side in males.

Tracheal volume of common eiders ranged 3.1–10.0 mm<sup>3</sup> in females, and

states, as applicable) were greater than for other variables (one-way ANOVAs,  $df = 1, 21, P < 0.001$  for both species).

**B** 

Mean bullar breadth and length in common eiders ( $n = 25$ ) were  $12.2 \pm 0.85$  (10.7–13.4), and  $23.3 \pm 0.80$  (range 22.1–24.7) mm, respectively. Corresponding values for king eiders ( $n = 25$ ) were  $9.90 \pm 0.44$  (9.18–10.7), and  $20.7 \pm 0.71$  (18.8–22.4). Relative bullar sizes (common/king) were thus 1.13 and 1.23, respectively, averaging larger than linear body-size differences between the species (Table 3).

Coefficients of variation (CVs) for bullar breadth and length were 3.41 and 7.01% for common eiders and 3.45 and 4.46% for king eiders (based on data above). By comparison, CVs for flattened wing length, culmen length, primary-9 length, and sternal-keel length, ranged from 4.08–6.91% in common eiders and 3.51–6.42% in king eiders (data in Table 1).

Bullar size was mainly negatively allometric in relation to body size in each species, but isometry or near-isometry was apparent for bullar length vs. wing length in both species and bullar breadth vs. head length in king eider (Table 5, Fig. 3). No positive allometry was found. Bullar size was absolutely larger in the larger species (common eider), but not relatively so:

1958, Johnsgard 1961a, Heinroth and Heinroth 1968, Livezey 1995).

Neither tracheal length (number of tracheal rings) nor size of tracheal rings increased with age. In some waterfowl species, the trachea grows in length over months ( and ; Würdinger 1970) to years (magpie goose, ; Johnsgard 1961a).

The trachea of some diving birds (e.g. alcids; EHM pers. obs.) is completely cartilaginous, hence collapsible when under pressure as during dives. In contrast, all stained eider specimens that we examined, including birds only ~3 months old, had fully ossified tracheae, ossified bullae, and cartilaginous bronchi, as is true of waterfowl generally (Wolff 1950, Mathey 1965). Hence the eider trachea cannot collapse. However, tracheal ossification is not universal even in Mergini (e.g., ; Humphrey 1955). Flexibility and extensibility of the eider trachea presumably are important in both underwater feeding and male displays, permitting the head and neck to be extended or moved quickly, and to assume display postures with the trachea curved or

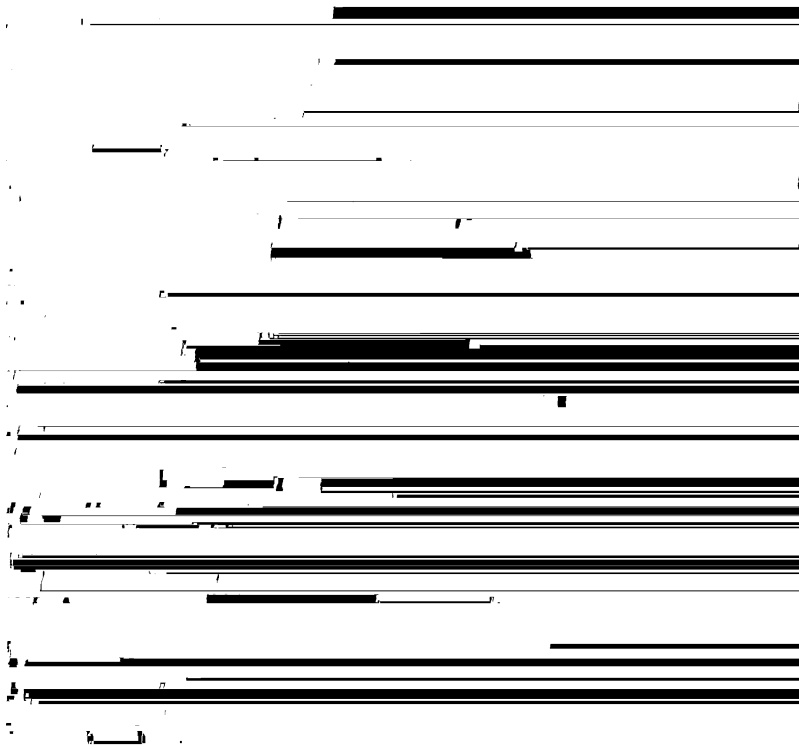


Fig. 2. Vocal muscles are larger on the left side and may be disproportionately larger in males than females of common eider and king eider : bivariate plots of size (left vs. right side) of for males and females of both species (fluid-preserved specimens). Lines of equality are shown for reference; numbers below each sex refer to number of observations above (left > right), on (left = right), or below (right > left) lines of equality. Solid symbols: king eiders; open symbols: common eiders.

Lalatta-Costerbosa et al. 1990, Ballintijn and Ten Cate 1997). Previous to our study, only Degner (1988) has shown that the vocal tract is relatively larger than body size in males than females. Further evidence for disproportionately larger vocal-tract structures in birds is in reports of larger size in the smaller sex of a few

species (Appel 1929, Miller 1934, Lockner and Youngren 1976, Clapperton 1986).

The role of in vocalization merits attention. We did not measure its thickness but it was clearly thicker in males. In the mallard and other waterfowl, this

Table 5. Summary of allometric (log-log) regressions of body variables on body size variables. Cell entries are: Slope<sup>1</sup> (95% CI; r<sup>2</sup>, n).

Regression variables	Common eider	King eider
Billar breadth (mm) vs. body mass (g)	0.11 (0.05–0.17; 0.38, 24)	0.08 () 196 258

structure thickens with age, a process related to



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## R

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