Articles

Allometry, bilateral asymmetry and sexual differences in the vocal tract of common eiders *Somateria mollissima* and king eiders *S. spectabilis*

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Intraspecific sexual differences, high variation, and positive allometry of sexually-selected external display structures are common. Many sexually-selected anatomical specializations occur in the avian vocal tract but intraspecific variation and allometry have been investigated little. The tracheal bulla *bulla syringealis* occurs in males of most duck species. We quantified variation and size-scaling of the bulla, plus sexual differences in size of trachea, bronchi, and vocal muscles, for 62 common eiders *Somateria mollissima* and 51 king eiders *S. spectabilis*. Trends were similar in both species. Bullar ossification and definitive size occurred early in life: bullar size did not differ between first-year and older males. Bullar size did not vary more than size of other body parts (CVs of 3.4–7.0% for bullar length and breadth). Bullar size scaled to body size with negative allometry or isometry. Vocal muscles were 10–50% thicker in males than females, a much greater sexual difference than in body size (CVs of 3–6% on linear body-size variables). Vocal muscles were larger on the left side in both sexes and bilateral asymmetry was slightly more pronounced in males. Low variation and a trend towards negative allometry suggest that bullar size is under stabilizing selection; if bullar size affects vocal attributes of voice, then the latter cannot be condition-dependent. We recommend comparative research on vocal communication, vocal individuality and vocal-tract anatomy and function in eiders and other ducks.

Patterns of variation in displays within and across species are important for understanding sexual selection and speciation (von Helversen and von Helversen 1994, Civetta and Singh 1999, Arnqvist and Rowe 2005). Displays and display structures typically differ across species, and often are sexually dimorphic and variable within species (Eberhard et al. 1998, Emlen and Nihout 2000, Miller and Burton 2001, Badyaev 2004, Emlen et al. 2005). Patterns of intraspecific variation and allometry vary according to function, however. Thus, high variation and positive allometry characterize many external display structures, yet low variation and negative allometry typify male genitalia, perhaps reflect-

ing constraints imposed by size of conspecific females; accordingly, condition-dependence cannot be expressed in the latter traits (Eberhard et al. 1998, Badyaev 2004, Hosken et al. 2005, Mutanen et al. 2006). At present, generalizations are difficult because only a few kinds of characters have been investigated; low variation and negative allometry may characterize internal structures in general because of needs for functional integration, for example. Information on sexually-selected internal non-genitalic structures may be particularly informative in this regard, such as those associated with vocal production in birds (Ames 1971, King 1989, Ballintjin et al. 1995, Fitch 1999, Fitch and Hauser 2003).

Anatomical specializations for generating or modifying sounds occur in the male vocal tract of many Anseriformes, a group in which vocal communication is important in courtship and competition for mates (Delacour and Mayr 1945, Johnsgard 1961a,b). The tracheal bulla (*bulla syringealis*; terms follow King 1993) on the left side of the lower trachea is present in most male Anatinae and presumably functions to generate sounds or modify syringeally-produced sounds (Rüppell 1933, Warner 1969, 1971, Lockner and Youngren 1976, King 1989, McLelland 1991, King 1993). Other bilateral asymmetry also is known in seaducks: tracheal displacement to the right side and larger bronchi and muscles on the left side (Rüppell 1933, Humphrey 1958, Phillips 1986, King 1989). The tracheal bulla is present in male eiders (*Somateria*; Fig. 1), so we took advantage of a collection of common *S. mollissima* and king *S. spectabilis* eiders, obtained for other purposes, to investigate vocal-tract variation and allometry. The bulla is a sexually-selected trait, so we postulated that: (1) bullar size would be more variable than size of other body parts, and (2) size of the tracheal bulla and other parts of the vocal tract would scale positively (exhibit positive allometry) on body size in males. Males are the most vocal sex, so we predicted also that (3) the vocal tract and vocal muscles would be relatively larger in males. Finally, we anticipated (4) bilateral asymmetry in syringeal muscles, with larger muscles on the left.
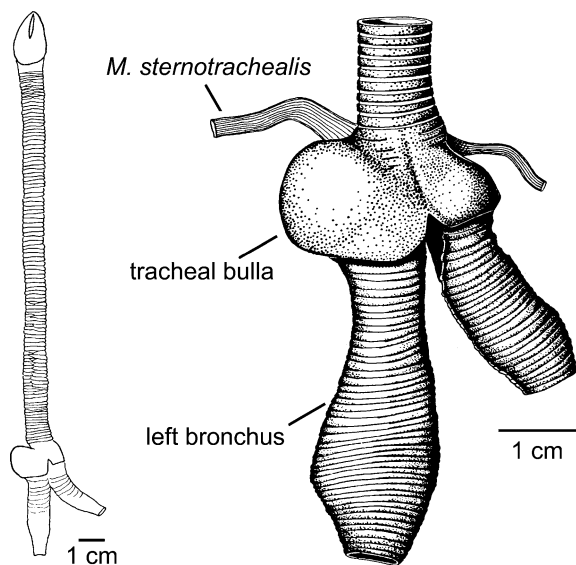

Fig. 1. Lower vocal tract of eiders (dorsal aspect): king eider *Somateria spectabilis* (left) and common eider *S. mollissima* (right). Note lack of trachea swellings, *bulla syringealis* on the left side, large left primary bronchus, and bilaterally asymmetric *Mm. sternotrachealis*. After Humphrey (1958: Fig. 1).

Methods

We studied 111 specimens of known age class (61 common eiders; 50 king eiders) plus two females of unassigned age class (one of each species; Table 1). One collection (East Bay, Southampton Island; 64° 00′N, 81° 15′W) was made in the breeding season and comprised only breeding adults. Some of these birds were captured on the nest then euthanized with CO_2, following guidelines of the Canadian Council on Animal Care; others were collected by shooting with a 12-gauge shotgun (shot size, no. 4). Other specimens were from outside the breeding season and were collected by shooting (as for the preceding) or died of natural causes: Cape Dorset (64° 15′N, 76° 30′W), Belcher Islands (56° 45′N, 79° 30′W), and Baffin Island (68°N, 71° W; Mallory et al. 2001). Carcasses were aged (most by SEJ) and dissected in the laboratory by staff or students of the Canadian Wildlife Service (CWS), University of New Brunswick (Fredericton) (UNB), Royal Ontario Museum (ROM), or Memorial University of Newfoundland (MUN), so specimens varied in quality (particularly completeness of tracheae and bronchi). Voucher specimens were deposited in the Royal Ontario Museum, Toronto, Ontario, Canada.

Birds were aged by plumage and length of bursa of Fabricius; females in adult plumage but with unconvoluted oviducts were considered to be immature (Jones et al. 1982, Mather and Esler 1999). Birds were aged as: first (hatching), second, or third year (HY, SY, TY, respectively); immature (IM, i.e. SY or TY); adult (AD, i.e. older than IM); or after-hatching-year (AHY). We tested for age effects across classes AD, IM, and HY with one-way ANOVAs. Following Bonferroni correction, only two variables showed significant age effects but trends were unsystematic: length of flattened wing was significantly shorter in HY male king eiders than in other age classes; and breadth of tracheal rings was significantly smaller in AD female common eiders. Therefore we combined age classes for further analyses. We followed the same procedure in determining lack of geographic variation in the sample.

Body measurements were taken by SEJ, M. Wayland (CWS), or M. Peck (ROM), following Dzubin and Cooch (1992). For analyses, we selected variables measured on most specimens: body mass (± 1 g); length of sternal keel (± 1 mm; taken on skinned carcasses, not on the defleshed and dried sternum as recommended by Dzubin and Cooch (1992)); length of flattened wing (± 1 mm); length of ninth primary (± 1 mm); length of head (± 0.1 mm); total tarsal length (± 0.1 mm); and length of culmen on midline (± 0.1 mm).

Vocal tracts were removed and preserved (Cannell 1988). Vocal tracts from one AD and one HY male and female of each species were cleared and stained for cartilage and bone to reveal calcified and cartilaginous

Table 1. Summary of information on common and king eider specimens collected in Nunavut, Canada, used in the study[1].

Species and specimen type	Date	Locality	Male			Female		
			AD	IM	HY	AD	IM	HY
Common eider:								
fluid-preserved	18–29 June 1999	Southampton Is.	12	0	0	12	0	0
fluid-preserved	4–10 November 1998	Belcher Is.	3	0	3	3	0	4
frozen	7–14 March and 17–18 May 2000	Belcher Is.	1	6	0	1	10	6
King eider:								
fluid-preserved	October 1999	Central Baffin Is.	3	4	16	4	4	12
frozen	12–15 February and 29 May 2001; 16 February 2002	Cape Dorset	1	1	0	2	1	2

[1]Two other birds were included: a female common eider of unknown age class, date, and locality; and a female king eider of unknown age class from Baffin Island. Abbreviations: AD =adult; IM =immature; HY =hatch year.

components (Cannell 1988). *M. cleidotrachealis* 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 (± 0.1 cc) on some common eider specimens by tying the larynx closed, inverting the trachea, and injecting the trachea with water at the tracheobronchial junction. Maximal tracheal length was measured (± 1 mm, with a ruler) from the cranial margin of the cranialmost tracheal ring to the caudal margin of the caudal-most tracheal ring, with the trachea fully stretched by hand. Minimal tracheal length was measured similarly, after fully compressing the trachea longitudinally by hand. Number of tracheal rings was counted (this total included individual elements contributing to partially fused rings). Breadth and craniocaudal length of tracheal rings were measured to ± 0.01 mm from ventral aspect, using digital calipers; rings 1 (closest to syrinx), 5, and 10 were measured. Rings were cleaned of membranes and muscles before they were measured. Maximal breadth and craniocaudal length of the *bulla syringealis* were measured to ± 0.05 mm with digital calipers. Breadth and craniocaudal length of the bronchial ring closest to the syrinx were measured to ± 0.01 mm using digital calipers. Additionally, maximal external bronchial ring breadth on left and right sides, and craniocaudal length at the point of maximal breadth were measured.

Dorsoventral and lateral dimensions of left and right *M. sternotrachealis* (breadth and height, hereafter) were measured ~ 0.5 cm from the muscle's syringeal insertion. For measurement, specimens were positioned with ventral side up, and the relaxed muscles were laid flat and extended perpendicular and lateral to the syrinx. Breadth and height of left and right *M. cleidotrachealis* were measured approximately 1 cm from insertion of the muscle on the trachea, with the specimen and muscles positioned as described. Breadth and height of left and right *M. tracheolateralis* were measured after severing the muscle approximately 1 cm from its origin

on the syrinx and dissecting it away from the trachea. Muscle measurements were made to ± 0.01 mm with a dissecting scope and ocular micrometer.

Many specimens had been preserved in fluid before receipt at MUN, so we investigated effects of fluid-preservation on measurement in a subsample of 16 common eiders. Specimens were measured (all variables; see above) fresh, then fixed in 5% formalin for 1 day, stored in 70% ethanol for 14 days, and remeasured. Paired t-tests revealed that preservation did not alter size of tracheal or bronchial rings but resulted in significant shrinkage of muscles (by 3–12%). As a result, measurements taken on fresh and fluid-preserved muscles were analyzed separately. To minimize measurement error and effects of distortion from preservation, we summed measurements on breadth and height of muscles for each specimen for analysis. Bullar measurements were highly repeatable ($>97\%$) so we did not quantify measurement error for purposes of comparing variation across traits.

Allometric (log-log) regressions of bullar variables on body-size variables were performed on males of each species. General linear model (GLM) analyses were used to investigate relative bullar size (bullar variables were dependent, and species plus body size were independent variables). GLMs also were used to test for effects of sex and side (right vs. left) on muscle size (as the dependent variable).

Results

General observations

Trachea, bulla, and syrinx were completely ossified and bronchi were completely cartilaginous in all stained specimens. *M. sternotrachealis* was a long (>40 mm) muscle that originated on the ventrocaudal extremity of the *Proc. craniolateralis* of the sternum, and inserted on the ventrolateral portion of the tympanum plus first (immobile) tracheal ring anterior to it. *M. tracheolateralis* originated on the anterior margin of the tympanum

slightly caudal and dorsal to that insertion. *M. cleidotrachealis* originated on the dorsal fascia of *M. pectoralis* ~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 *saccus clavicularis*, whose inner surface was covered by a thin sheet of muscle; *M. cleidotrachealis* inserted on the sides of the trachea just caudal to and in close association with the cranial edge of the *saccus clavicularis*. The trachea emerged from the *saccus clavicularis* 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.

Mem. tympaniformis medialis was thicker in males than females, and was thicker on the left side in males.

Tracheal volume of common eiders ranged from 4.0–7.4 cc (mean ± SD = 5.42 ± 1.12; n = 13), and was not correlated with either body mass or length of flattened wing (r = 0.10 and 0. 01, respectively). Sample sizes were too small to test for age or sex effects.

Tracheae were highly extensible (Table 2), by ~90% in common eiders (extended/compressed for females = 1.90 ± 0.14 and for males, 1.93 ± 0.21), and ~120% in king eiders (females: 2.18 ± 0.09; males: 2.19 ± 0.10; sample sizes in Table 2). Elastic membranes between rings permitted high tracheal flexibility, but tracheal rings were completely ossified so cross-sectional shape was fixed.

No relationships between tracheal length and number of tracheal rings were significant when sexes were analyzed separately. When combined, two significant correlations were found: total number of rings and length of extended trachea (common eider (n = 24:

r = 0.44, P = 0.03; king eider (n = 10: r = 0.67, P = 0.04); and lengths of extended and compressed tracheae (common eider: r = 0.33, P = 0.11, n = 24; king eider, r = 0.65, P = 0.04, n = 10).

Variation between sexes

The common eider was the larger species and males were the larger sex within each species, with sexual differences (male/female means; M/F hereafter) in linear body measurements averaging 1.03 ± 0.034 (n = 7 variables) for common eiders and 1.04 ± 0.028 for king eiders (Table 3). Sexual differences were similar in magnitude in: number of tracheal rings, tracheal length, and size of tracheal rings (numbers 10, 15) distant from the syrinx (n = 8 variables; common eider: 1.03 ± 0.03; king eider: 1.04 ± 0.03). In contrast, M/F estimates for breadth of tracheal ring 5 were larger than body-size M/F measures in both species (M/F = 1.08 and 1.11 in common and king eiders, respectively), as were both variables on ring 1 (mean, 1.10; range, 1.07–1.12; Table 2). Overall, the four M/F measures on rings 1 and 5 were greater than other tracheal variables plus body-size variables for king eider (P = 0.03), but not common eider (P = 0.07; one-way ANOVAs, df = 1, 15).

Size differences between sexes were even greater for bronchial and muscular variables: M/F averaged 1.19 for left-bronchial variables (1.12 for right) across species, and 1.11 (left) and 1.10 (right) for *M. tracheolateralis* (Table 4). M/F values for *M. sternotrachealis* were larger: 1.53 (left) and 1.28 (right) (Fig. 2). Sexual differences in size of *M. cleidotrachealis* also were large (common eiders only): M/F = 1.21 (left), 1.35 (right). Overall, M/F estimates for bronchial and muscular variables (using median values for left plus right sides, and across frozen or fluid-preserved

Table 2. Descriptive statistics for tracheal variables for common eider and king eider specimens used in the study (age classes combined; see text). Data are shown as mean ± SD, in mm (except for numbers of tracheal rings).

Variable	Common eider			King eider		
	Females (F)	Males (M)	M/F	Females	Males	M/F
No. tracheal rings:	n = 17	n = 7		n = 6	n = 4	
Total[1]	105 ± 4.2	108 ± 5.3	1.03	103 ± 5.4	100 ± 6.0	0.97
Syrinx to air sac[2]	25.4 ± 3.16	26.0 ± 2.89	1.02	21.2 ± 4.07	22.5 ± 1.29	1.06
Tracheal length:	n = 17	n = 7		n = 6	n = 4	
Extended	222 ± 7.6	231 ± 9.6	1.04	194 ± 6.3	196 ± 15.2	1.01
Compressed	117 ± 9.7	121 ± 12.0	1.03	89.3 ± 4.80	89.2 ± 3.59	1.00
Tracheal ring: 1	n = 33, 32	n = 24		n = 21	n = 21	
Height	6.63 ± 0.436	7.11 ± 0.611	1.07	5.33 ± 0.582	5.95 ± 0.643	1.12
Breadth	8.50 ± 0.506	9.40 ± 0.551	1.11	8.16 ± 0.404	9.18 ± 0.436	1.12
Tracheal ring: 5	n = 32	n = 23		n = 19	n = 20	
Height	5.95 ± 0.567	5.92 ± 0.446	0.99	4.75 ± 0.562	4.78 ± 0.519	1.01
Breadth	7.77 ± 0.481	8.42 ± 0.548	1.08	7.78 ± 0.512	8.61 ± 0.694	1.11

Table 3. Sexual-size dimorphism and descriptive statistics for body-size variables for common eider and king eider specimens used in the study (age classes combined; see text). Data are shown as mean±SD (n), in mm or $g^{1/3}$ (the latter for body mass$^{1/3}$).

Variable	Common eider			King eider		
	Females (F)	Males (M)	M/F	Females	Males	M/F
Body mass$^{1/3}$*	13.2±0.38 (36)	12.9±0.86 (24)	0.98	11.4±0.36 (22)	11.8±0.27 (19)	1.04
Head length	122±2.9 (24)	127±4.0 (12)	1.04	104±4.78 (18)	109±2.7 (21)	1.05
Flattened wing length	295±11.1 (36)	299±12.2 (23)	1.01	261±9.96 (25)	271±9.5 (25)	1.04
Tarsal length	66.1±2.09 (17)	68.1±2.62 (11)	1.03	56.4±2.56 (20)	57.9±1.72 (21)	1.03
Culmen length	50.6±3.18 (30)	53.7±3.71 (23)	1.06	33,1±2.00 (12)	33.8±2.17 (17)	1.02
P9 length	186±9.2 (18)	191±9.44 (10)	1.03	160±9.9 (20)	164±8.6 (21)	1.02
Sternal keel length	137±2.8 (17)	143±7.4 (11)	1.04	118±3.64 (12)	125±5.7 (17)	1.06
Tracheal ring: 10	n=32	n=24		n=20	n=22	
Height	5.69±0.609	5.77±0.403	1.01	4.76±0.406	4.94±0.536	1.04
Breadth	7.75±0.535	8.13±509	1.05	7.82±0.537	8.54±0.690	1.09
Tracheal ring: 15	n=32	n=24		n=18	n=22	
Height	5.51±0.539	5.64±0.392	1.02	4.85±0.388	4.97±0.649	1.02
Breadth	7.98±0.560	8.18±0.473	1.02	8.02±0.357	8.74±0.747	1.09

*For body mass (g): common eider females, 2316±190 and males, 2184±441; king eider females, 1500±141 and males 1652±111.
[1]Ranges: common eider females 98−113, males 99−114; king eider females 96−111, males 96−109.
[2]Ranges: common eider females 19−30, males 22−30; king eider females 15−26, males 21−24.

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

Bullar size, variation, and allometry

Mean bullar breadth and length in common eiders (n = 25) were 12.2±0.85 (10.7−13.4), and 23.3±0.80 (range 22.1−24.7) mm, respectively. Corresponding values for king eiders (n = 25) were 9.90±0.44 (9.18−10.7), and 20.7±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: interaction terms were not significant in GLM analyses (P = 0.9 and 0.8 for bullar breadth and width, respectively).

Bilateral differences in bronchial and muscle size

GLM analyses revealed that size of bronchi and muscles differed between the sexes and between left and right sides (Table 4). There was also a suggestion of disproportionately greater bilateral asymmetry in males: interaction terms [sex × side] for *M. sternotrachealis* were close to significance (P = 0.06 for each species) and for *M. tracheolateralis* were P = 0.04 (common eider), and 0.5 (king eider; Fig. 2). Trends were similar for both fresh and fluid-preserved muscles.

Parallel GLM analyses with bronchial variables as dependent variables resulted in nearly identical trends in sexual and bilateral differences, with a suggestion of relatively larger left bronchi in males than females (data not presented).

Discussion

General observations

The vocal tract of common and king eiders conforms to the general seaduck pattern. The trachea is uniform in diameter, except is slightly larger near the bulla, and it lacks specialized swellings such those of other Anatinae, including Mergini (Fig. 1). Delacour and Mayr (1945) stated that tracheal diameter is variable in eiders, but this appears to be the case only for *Polysticta* (Johnsgard 1960). The tracheal bulla of eiders also is fairly simple and conservative, differing across the four extant species most obviously in size (smallest in *Polysticta* and *S. fischeri* and largest in *S. mollissima*: Humphrey

Table 4. Summary of descriptive statistics for bilateral variables on bronchi and muscles of common eider and king eider specimens used in the study. Data are shown as mean±SD (n), in mm[1].

Variables[2]	Females (F)			Males (M)			M/F[4] (L, R)
	Left side (L)	Right side (R)	L/R[3]	Left side	Right side	L/R[3]	
Common eider:							
BR 1	12.4±1.04 (32)	12.5±0.95 (32)	1.00	14.7±0.94 (24)	14.0±1.17 (24)	1.06	1.19, 1.12
BR max.	15.9±0.97 (27)	12.0±1.06 (25)	1.32	19.8±1.44 (21)	13.2±1.43 (21)	1.44	1.25, 1.10
King eider:							
BR 1	10.6±0.82 (21)	10.4±0.88 (21)	1.01	12.6±1.14 (20)	12.5±0.98 (22)	1.05	1.19, 1.20
BR max.	14.4±0.65 (16)	11.5±0.97 (17)	1.05	16.4±1.37 (16)	12.3±0.93 (13)	1.36	1.14, 1.07
Common eider:							
MS (Z)	2.92±0.474 (17)	2.92±0.341 (17)	1.02	4.45±0.438 (7)	3.92±0.388 (7)	1.14	1.52, 1.34
MS (P)	2.85±0.394 (19)	2.66±0.494 (19)	1.09	4.41±0.624 (18)	3.79±0.434 (18)	1.17	1.55, 1.42
MT (Z)	3.94±1.000 (20)	3.61±0.775 (19)	1.16	4.26±0.771 (18)	3.60±0.665 (17)	1.18	1.08, 1.00
MT (P)	3.86±0.625 (17)	3.38±0.602 (17)	1.11	4.19±0.490 (7)	3.56±0.605 (7)	1.19	1.09, 1.05
CT (Z)	6.20±1.154 (6)	6.07±1.252 (5)	1.02	7.48±0.735 (2)	8.22±0.940 (2)	0.91	1.21, 1.35
King eider:							
MS (Z)	2.99±0.171 (6)	2.64±0.256 (6)	1.14	4.08±0.283 (4)	3.18±0.780 (4)	1.33	1.36, 1.20
MS (P)	2.26±0.290 (20)	2.24±0.300 (18)	1.03	3.79±0.742 (19)	3.30±0.650 (20)	1.04	1.68, 1.17
MT (Z)	3.70±0.421 (6)	3.11±0.476 (6)	1.21	4.34±0.328 (4)	3.63±0.689 (4)	1.21	1.17, 1.17
MT (P)	3.37±0.438 (19)	2.95±0.520 (18)	1.16	3.69±0.809 (19)	3.46±0.594 (15)	0.97	1.09, 1.17
MC (Z)	5.13±0.872 (5)	5.26±1.207 (6)	0.84	5.15±0.610 (4)	5.63±1.032 (4)	0.92	1.00, 1.07

[1]The two measurements for each structure were summed (e.g., breadth+height of the first bronchial ring; see Methods).
[2]Abbreviations: BR, bronchial ring; MS, *M. sternotrachealis*; MT, *M. tracheolateralis*; MC, *M. cleidotrachealis*; P, preserved in fluid; Z, frozen specimen, measured after thawing.
[3]These values represent means of (L/R) for individual specimens, not grand means based on mean values in this table.
[4]Grand means of mean values in this table are shown.

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 (*Anser* and *Branta*; Würdinger 1970) to years (magpie goose, *Anseranas semipalmatus*; 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., *Bucephala*; 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 bent in various ways (McKinney 1961, Johnsgard 1964, McKinney 1965, Palmer 1967, Cramp 1977, McLelland 1989, Suydam 2000). Greater tracheal extensibility in male common goldeneye *Bucephala clangula* than in Barrow's goldeneye *B. islandica* may be adaptive for the former's more extreme neck-stretching in displays

(Latham and Romsey 1798, Humphrey 1955, Johnsgard 1961a, Heinroth and Heinroth 1968, Eadie et al. 1995, 2000). Tracheal extensibility in Mergini has been quantified only by Beard (1951): one relaxed trachea of a male hooded merganser *Lophodytes cucullatus* was stretched by 41% (from 110 to 155 cm). High tracheal extensibility therefore appears to be widespread in Mergini and may be important in affecting sound properties related to tracheal length (Fitch 1999, Fitch and Hauser 2003).

Sexual-size dimorphism

Sexual differences in body size of waterfowl have been discussed extensively (Livezey and Humphrey 1984, Livezey 1995, Figuerola and Green 2000). We found differences in size of the vocal tract (e.g. ∼20% in left-bronchial size), and vocal muscles (e.g. ∼50% in size of left *M. sternotrachealis*) to be greater than differences in body size, suggesting an increase in size in males under the influence of sexual selection. Functional interpretation of this finding in terms of sexual differences in vocalizations and vocal activity must await study of vocal communication in the species.

Many accounts suggest that males have larger vocal tracts or vocal-tract structures in species where males are the larger sex (Stresemann 1927, 1937, Gullion 1950, Warner 1971, Lockner and Youngren 1976,
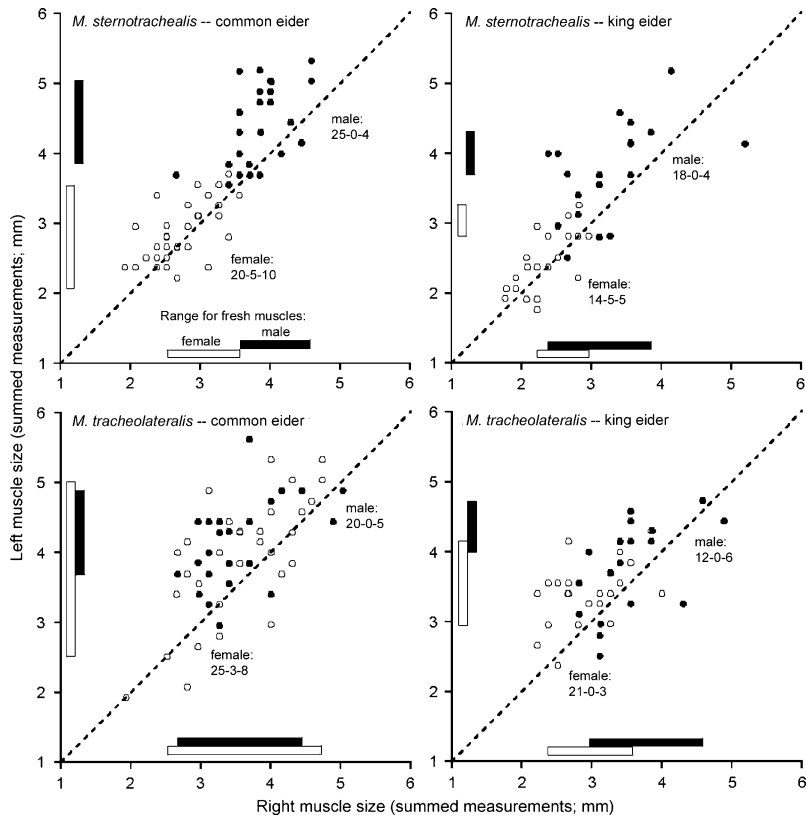
Fig. 2. Vocal muscles are larger on the left side and may be disproportionately larger in males than females of common eider *Somateria mollissima* and king eider *S. spectabilis*: bivariate plots of size (left vs. right side) of *M. sternotrachealis* and *M. tracheolateralis* for males and females of 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 *Mem. tympaniformis medialis* in vocalization merits attention. We did not measure its thickness but it was cleary thicker in males. In the mallard *Anas platyrhynchos* and other waterfowl, this

Table 5. Summary of allometric (log-log) regressions of bullar variables on body-size variables. Cell entries are: Slope[1] (95% CI; r^2, n).

Regression variables	Common eider	King eider
Bullar breadth (mm) vs.:		
body mass (g)	0.11 (0.05–0.17; 0.38, 24)	0.08 (−0.10–0.26; 0.04, 22)
wing length (mm)	0.49 (0.16–0.82; 0.31, 23)	0.44 (0.06–0.82; 0.18, 28)
head length (mm)	0.33 (−0.27–0.93; 0.13, 12)	0.68 (0.09–1.27; 0.21, 24)
culmen length (mm)	0.29 (0.09–0.49; 0.30, 23)	–
Bullar length (mm) vs.:		
body mass (g)	0.07 (−0.08–0.22; 0.04, 24)	0.08 (−0.23–0.39; 0.01, 22)
wing length (mm)	0.59 (−0.15–1.33; 0.12, 23)	0.62 (0.07–1.17; 0.17, 28)
head length (mm)	0.96 (−0.30–2.22; 0.22, 12)	−0.33 (−1.28–0.62; 0.02, 24)
culmen length (mm)	0.12 (−0.32–0.56; 0.01, 23)	–

[1]Isometric slope = 1/3 for body mass and 1 for other variables.
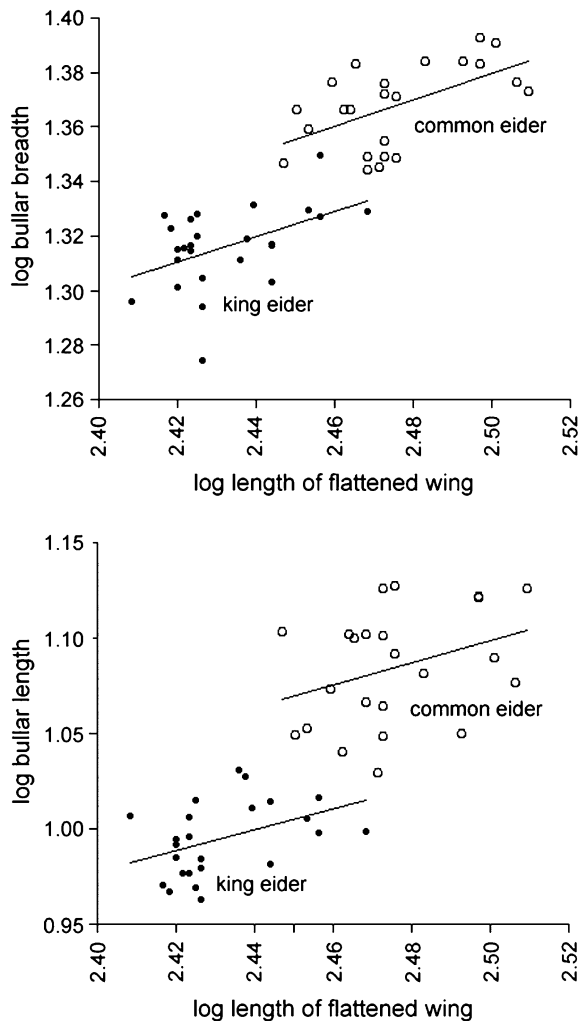
Fig. 3. Bullar size in male common eider *Somateria mollissima* and king eider *S. spectabilis* increases roughly in proportion to body size or slightly less, within and between species: allometric plots of bullar breadth and height on body size (length of flattened wing). Regression lines are shown; for statistical details, see Table 5. Solid symbols: males; open symbols: females.

structure thickens with age, a process related to developmental breaking of the voice (Lockner and Youngren 1976, Abs 1980).

Bullar variation and allometry

Bullae of eiders killed in the fall did not differ in size from those of adults, so adult bullar size must be reached early in life. Bullar growth begins early in embryonic development in the mallard, and presence of the bulla can be used to sex downy young of many anatid species, including seaducks (Broman 1942,

Wolff 1950, Beer 1963). Anatid vocal development takes place over a longer period, so roles of the bulla in vocalization and vocal development must be complex.

We found no published data on mensural variation in the trachea or syrinx of birds. Contrary to expectation, variation in bullar size was low and similar to variation in body-size variables. Asymptotic growth early in life, coupled with low variation in size, explain the observed scaling patterns of mainly negative allometry of bullar size in relation to body size. Taken together, these observations are consistent with low variation that reflects stabilizing selection for bullar size. This could result from the need for the bulla to function in concert with other parts of the vocal tract, or because bullar size affects vocal attributes which themselves are under stabilizing selection. Finally, relative bullar size was similar in both species. The other two eider species have smaller bullae but both species are smaller in body size, so whether their bullae are relatively smaller is an open question.

Bilateral asymmetry

We observed pronounced bilateral asymmetry in the lower vocal tract of common and king eiders of both sexes. Wolff (1950) detected bilateral asymmetry in syringeal cartilages of embryonic mallards of both sexes. For *Somateria*, we observed the left bronchus to be larger, and the left *M. sternotrachealis* thicker than the right (Rüppell 1933). In contrast, the relatively silent *Polysticta* has a small bulla and its bronchi plus *M. sternotrachealis* are similar in size on right and left sides (though the latter muscle is very thick; Humphrey 1955, 1958, Johnsgard 1961a,b, Livezey 1995).

Patterns of bilateral asymmetry in bronchi of other non-passerine taxa are highly variable. For example, the right bronchus is larger than the left in many non-passerines (Rüppell 1933, Ames 1971, King 1989, Ballintijn et al. 1995, Ballintijn and ten Cate 1997). Similar variability occurs in bilateral asymmetry of vocal muscles (Beddard 1898, Warner, 1969, 1972, Gaunt et al. 1982, King 1989, Ballintijn et al. 1995), and the right *M. sternotrachealis* is absent altogether in the blue-and-yellow macaw *Ara ararauna* (King 1989). In the face of such high variability, patterns of asymmetry within specific clades such as Anatidae are likely to be most informative.

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