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Syringeal anatomy and allometry in murres (Alcidae: *Uria*)

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Abstract Species and sexual differences in vocalizations and the vocal tract are widespread. We studied the vocal tract of Common (*Uria aalge*) and Thick-billed (*U. lomvia*) Murres. We predicted anatomical or allometric differences in adults between species and sexes due to vocal differences related to social behavior (Common Murres nest at higher densities; males are the more aggressive sex, etc.). The vocal tract was anatomically simple and similar between species and sexes. The trachea was mainly cartilage, but the posteriormost 4–6 tracheal rings were calcified and fused as the tympanum, as part of the syrinx. The syrinx included the (unfused) first bronchial semirings, which were enlarged and calcified beneath the insertion of *M. tracheolateralis*. Weak bilateral asymmetry (right side larger) occurred in widths of *M. tracheolateralis* and *M. sternotrachealis*. The trachea was ~10% longer in Common Murres; the tympanum and *M. sternotrachealis* width were relatively larger in Thick-billed Murres. Vocal-tract morphology and size did not differ between the sexes in either species. In allometric analyses on adults, isometry characterized (1) tympanum size in relation to head + bill length, and to humerus length (respectively), in Thick-billed Murres, and (2) *M. sternotrachealis* width in relation to tarsometatarsal length in both species. Comparative field studies on species and sexes are needed to clarify the functional significance of our findings in relation to vocalization.

Keywords Allometry · Anatomy · Sexual dimorphism · Syrinx · *Uria*

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Introduction

Many specializations for sound production in birds (e.g., increased size or special structures; King 1989) have been shaped by sexual selection, and have diverged between related species (Fitch 1999; Edwards et al. 2005; Price 2007). Many specializations are also more developed in or limited to one sex: tracheal modifications in male ducks; esophageal air sacs in male grouse; etc. However, the syrinx is anatomically complex and interspecifically diverse even in species that lack special structures, so syringeal morphology has proven to be informative in many systematic studies (Lanyon 1986; Prum 1992; Griffiths 1994a, b; Gaban-Lima and Höfling 2006).

High interspecific variation suggests that social selection promotes divergence in the sound-production apparatus generally. This may also apply within species: vocal-tract size or morphology may differ between the sexes in species with sexual differences in vocalizations used in mate attraction, territoriality, or parental care. The male syrinx is larger in many species (Häcker 1900; Wade and Buhlman 2000; Veney and Wade 2004). Furthermore, sexual differences occur in both size of the vocal apparatus and vocalizations in various non-passerines, including Anseriformes (Warner 1971; Lockner and Youngren 1976; Lalatta-Costerbosa et al. 1990), Columbiformes (Ballintijn and Ten Cate 1997), Galliformes (Bottino et al. 2006);

Ralliformes (Gullion 1950), and Turniciformes (Balthazart et al. 1983).

The prediction of parallel morphological and vocal differences between the sexes seems to be met by the examples just listed. However, males are the larger sex in all those taxa, so would be expected to have larger vocal tracts than females for that reason alone. Nevertheless, scattered evidence suggests that relative size differences are widespread: males are smaller but have larger syringeal skeletons and deeper voices in Strigidae (Miller 1934); male and female Jungle Crows (*Corvus macrorhynchos*) are similar in body size, but males have a longer trachea (Tsukahara et al. 2006), etc. Allometric analyses that control for sexual differences in body size are necessary to investigate this matter properly (Degner 1988; Miller et al. 2007).

In grouse *Dendragapus* and eiders *Somateria*, males have a relatively larger vocal tract than females (Degner 1988; Miller et al. 2007). Both taxa exhibit sexual dimorphism in plumage, size, and behavior, and males have an anatomically specialized vocal tract, so disproportionate vocal-tract size differences between the sexes may not be surprising. Are vocal differences between species or sexes correlated with anatomical or size differences in vocal tracts, in species that lack specialized structures, or in which sexes are similar in size? In this paper, we report on two size-monomorphic species of Charadriiformes, a group characterized by an anatomically simple and conservative syrinx (Warner 1969; King 1989; Brown and Ward 1990).

We describe syringeal anatomy and static allometry (Cock 1966) in adult male and female Common (*Uria aalge*) and Thick-billed (*U. lomvia*) Murres. Common Murres typically nest in high densities and interact frequently with many different birds, whereas Thick-billed Murres nest on narrow ledges so interact less often, and with many fewer individuals (Cramp 1989; Gaston and Hipfner 2000; Ainley et al. 2002). Despite these differences, no vocal differences between the species have been documented (Schommer and Tschanz 1975; Cramp 1989; Tschanz 1968; Lefevre et al. 2001). Males arrive at colony sites earlier than females each spring, and engage in much aggressive behavior in relationship to nest-site procurement and defence, then and throughout the nesting period (Cramp 1989; Gaston and Hipfner 2000; Ainley et al. 2002). The greater participation of males in aggressive behavior may explain their larger bills and skulls (Livezey 1988; Stewart 1993). Thick-billed Murres appear to be the more aggressive of the two species (Tuck 1961). The sexes differ in parental behavior as well; for example, males almost always accompany the chick to sea (Paredes et al. 2006). Behavioral differences between the species and sexes may be accompanied by vocal differences, but the matter has not been investigated.

Methods

Specimens and measurements

Specimens originated from British Columbia, Alaska, the central Canadian Arctic, western Greenland, and Newfoundland and Labrador. They were contributed by various individuals and agencies (see "Acknowledgements"). For analysis we lumped samples as: Atlantic (Newfoundland: Common Murre only: $n = 33$); Atlantic–Arctic (Newfoundland, Nunavut, Greenland: Thick-billed Murre only: $n = 62$); or Pacific (British Columbia and Alaska: Common Murre, $n = 41$; Thick-billed Murre, $n = 18$).

We judged Atlantic specimens to be in their first year of life ("juvenile", hereafter) or later ("adult"), based on plumage and skull characters (Gaston 1984; Nevins and Carter 2003). Some specimens were collected as breeding adults, or were labeled as juvenile or adult, based on unknown criteria. Specimens of unknown age that had been collected from May to July were judged to be adults.

Measurement data were variable and of variable quality, so we analyzed only our own measurement data for specimens from Nunavut, Greenland, and Newfoundland. We measured: (1) body mass (to ± 1 g); and (2) head + bill length (to ± 1 mm), from the tip of the bill to the posteriormost point on the back of the head (Howes and Bakewell 1989). As proxies for postcranial body size, we measured (to ± 1 mm) length of (3) humerus, (4) femur, and (5) tarsometatarsus, after dissecting them out of specimens. Head + bill length was excluded from some analyses, because we confirmed that it is relatively larger in males (Livezey 1988).

We measured (to ± 1 mm) length of the vocal tract in situ, with the bird on its back with neck extended: distance from the tracheobronchial junction to where the trachea crossed the plane of the posterior surface of the lower mandibles. We estimated tracheal extensibility in some Thick-billed Murres from Greenland. We dissected out the vocal tract, and measured its length (to ± 1 mm) when it was compressed longitudinally to minimal length. We measured (to ± 1 mm) extended length as follows: we looped cotton thread around the tympanum (terms follow King 1993) just anterior to its widest point, tied the other end to a Pesola #20100 100-g spring scale (Pesola, Baar, Switzerland), and stretched the trachea until a tension of 20 g was reached.

Vocal tracts were dissected from fresh or thawed specimens and stored in 75% ethanol (Cannell 1988). Subsequently, 32 specimens (2 adults of each sex, for each species, for each geographic region) were stained for cartilage and calcium phosphates, and then stored in 90% glycerin (Cannell 1988).

To estimate effects of fixation and fluid preservation on measurements, we fixed 32 fresh common and 16 fresh Thick-billed Murre specimens in 10% formalin for 4 days after measurement, transferred them to 75% ethanol for 14 days, and then re-measured them. Measurements decreased by 2.9% for syringeal width, 10.1% for thickness of *M. tracheolateralis*, and 12.9% for thickness of *M. sternotrachealis*. These figures were used as correction factors for fluid-preserved specimens.

Gross measurements of unstained specimens were taken (± 0.1 mm) with a dissecting microscope (10×) and ocular micrometer. Measurements were taken on: dorsoventral depth of syrinx, on both sides; width of syrinx (dorsal aspect); maximal width of *M. sternotrachealis* and *M. tracheolateralis* on both sides, just anterior to the latter's origin on the first bronchial semiring. We noted visually whether *M. sternotrachealis* inserted asymmetrically.

We tested for sexual-size differences for each species in each region with MANOVA (head + bill length included or excluded). Univariate allometric analyses were carried out using ordinary least-squares regression (log-log), with syringeal variables as response variables, and body-size variables as predictor variables.For comparison of size-scaling between species, we used general linear models, with syringeal variables as response variables, and species plus body-size variables as predictor variables (head + bill length included and excluded). No interaction terms were significant in any analysis, so were dropped, and analyses re-run. Trends and interpretations were uniform across analyses, so we report only on results of single-variable analyses.

For statistical analyses we used JMP IN 5.1 (SAS Institute, Cary, North Carolina) and SPSS 15.0 (SPSS, Chicago, Illinois). We deposited voucher specimens in the Newfoundland Museum (St John's) and Royal Ontario Museum (Toronto).

Results

General description

The trachea was cartilaginous, and could be collapsed completely by squeezing between the fingers. In the anteroposterior dimension, tracheal rings were smallest at the anterior end of the trachea and largest at the posterior end. Rings were separated completely from one another by highly elastic membranes. Rings were notched dorsally and ventrally, and successive rings partly overlapped, alternately overlapping and being overlapped, on left and right sides (Fig. 1). In cross section, the trachea was slightly elliptical and larger anteriorly, but from mid-trachea to the tympanum was ~circular (Fig. 2a). At the tympanum, the pessulus marked an abrupt change from the circular trachea to strongly elliptical entrances to the bronchi (Fig. 2b, c). The second bronchial semiring was sharply inset relative to the first semiring, so bronchial lumina were most extremely elliptical at that point (Fig. 2b, c).

Posteriormost tracheal rings were fully calcified: first to third rings in all Common Murres, and first plus second rings in all Thick-billed Murres; the first to fourth rings were calcified extensively in both species (Fig. 1). A few specimens showed no calcification anterior to the fifth (Common Murre) or fourth (Thick-billed Murre) tracheal rings; the median anteriormost ring with calcification was the sixth or seventh, respectively. The trachea was almost entirely cartilaginous anterior to the tympanum, although tiny calcified patches occurred up to the 10th (Common Murre) or 19th (Thick-billed Murre) rings (Fig. 1). No sexual differences in calcification were apparent.

Three to five tracheal rings were fused ventrally, and usually one more than that number were fused dorsally; some lateral fusion occurred also (Fig. 1). Thus, four to six tracheal rings constituted the tympanum, with a tendency for a greater number in Common Murre: counts of four, five, and six rings were 4-11-1 for Common Murre, and 10-3-3 for Thick-billed Murre. The first bronchial semiring can be considered as a *Cart. bronchosyringealis* because it was substantially modified, being very large, overlapping the first tracheal ring, and usually (13/16 Common Murres, 14/16 Thick-billed Murres), with calcification within an anteriorly expanded portion, beneath the insertion of *M. tracheolateralis* (Fig. 1c). This semiring was mobile, and able to be moved anteriorly considerably to overlap the tympanum. The second bronchial semiring differed slightly from more posterior semirings, in being weakly bowed anteriorly (Fig. 1c); otherwise, no semirings posterior to the first one were modified. No sexual differences were apparent.

Mem. tympaniformis medialis was the only potentially vibratile membrane present; it was thick and cartilaginous anteriorly (Fig. 1b, d). This membrane was bounded by the widely separated ends of the bronchial semirings, and (anteriorly) by the pessulus. Sometimes, the dorsal ends of the first two tracheal rings contacted the pessulus dorsally, so the tympanum and pessulus were separated by a membranous region in that area (Fig. 1b). The pessulus was calcified and fused with the tympanum dorsally and ventrally on the midline, extending obliquely from a more posterior position ventrally, to a more anterior position dorsally (Fig. 1d).

M. sternotrachealis originated on *Proc. craniolateralis* of the sternum, and inserted laterally on the trachea ~1–2 cm posterior to its emergence from the *Saccus interclavicularis*. *M. tracheolateralis* inserted on the first bronchial semiring. The insertion was slightly dorsal to the midline,

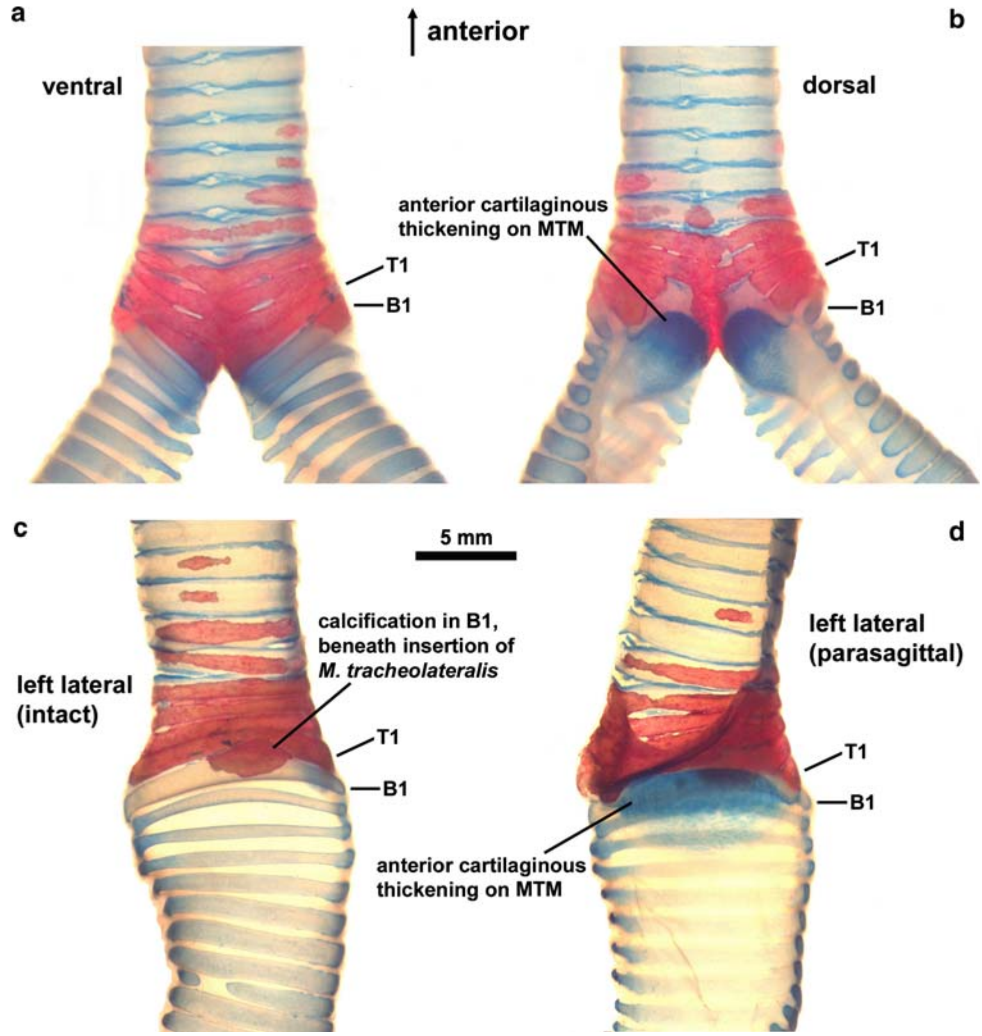

Fig. 1 General anatomy of the vocal tract of murres (*Uria lomvia* is shown). Cartilage is shown as *blue*, and calcified parts are shown as *red*. *MTM* medial tympaniform membrane (*Mem. tympaniformis medialis*); *T1* first tracheal ring; *B1* first bronchial semiring. In this specimen, the tympanum comprised tracheal rings T1–T4 (in most specimens, one more tracheal ring was fused dorsally than ventrally), of which T1 and T2 were separated from the pessulus dorsally by a membranous area. Note: (1) the large calcified area on B1 in Fig. 1c (also visible through the anterior margin of the membranous area in Fig. 1d); and (2) the scattered islands of calcification on tracheal rings anterior to the tympanum

on the anteriorly expanded part of the semiring; the area of insertion on this process usually was marked by localized calcification, which was sometimes extensive (Fig. 1c).

In situ length of the vocal tract did not differ in length between age groups or between sexes (one-way ANOVAs, $P > 0.05$) (mean ± SD): Common Murre, male 137 ± 1 mm ($n = 10$) and female 134 ± 1 mm ($n = 18$); Thick-billed Murre, male 124 ± 1 mm ($n = 22$) and female 122 ± 2 mm ($n = 15$). However, vocal-tract length differed between species: Common Murre, 135 ± 5 mm ($n = 32$); and Thick-billed Murre, 124 ± 7 mm ($n = 42$) (one-way ANOVA, $P < 0.0001$). Tracheal rings numbered 82–100 (median, 93; $n = 14$) in Thick-billed Murres, of which 21–34 (median, 26; $n = 12$) were situated between the tympanum and where the trachea emerged from the *Saccus cervicalis* (in both species, the distance from the latter landmark to the tracheobronchial junction was ~3–5 cm). Also in Thick-billed Murre, each bronchus had 16–28 (median, 22) semirings ($n = 13$ for left and 7 for right bronchi), and the number was correlated between sides: numbers of left and right semi-rings in six birds were 16-16, 20-20, 21-22, 22-22, 22-23, and 28-28 (Pearson's product-moment correlation coefficient $r = 0.99$, $P < 0.01$). Finally, the trachea of this species was fairly extensible: extended length was 57–78% (median, 67%) greater than compressed length ($n = 13$).

Bilateral asymmetry

No bilateral asymmetry was measured for syringeal depth in either species (Wilcoxon's matched-pairs tests; $P > 0.05$). However, weak bilateral asymmetry was detected for muscles, with the right side being slightly larger (matched-pairs tests): *M. sternotrachealis* in Common Murres ($n = 70$; $P = 0.02$); and *M. tracheolateralis* in Thick-billed Murres ($n = 52$; $P = 0.01$). Size of structures on left and right sides was positively correlated; *r*-estimates for Common Murres and Thick-billed Murres (respectively) were: syringeal depth, 0.88 and 0.94; *M. sternotrachealis*, 0.72 and 0.70; and *M. tracheolateralis*, 0.44 and 0.57

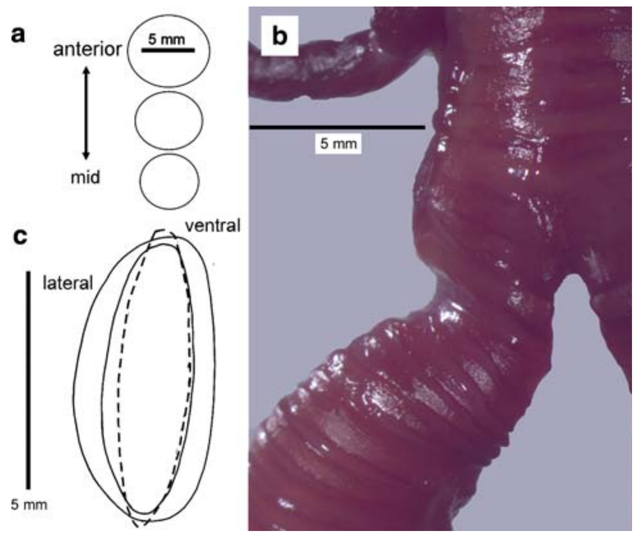

Fig. 2 General configuration of tracheal and bronchial lumina in murres (*Uria lomvia* is shown). **a** Cross-sectional tracheal shape and size changed little along the length of the trachea. Cross sections are shown from *anterior* to *posterior*, beginning (*top*) ~10 rings posterior to the larynx to (*bottom*) mid-trachea; the central cross section is midway between those points. Shape and size did not change from mid-trachea to about the fifth tracheal ring (T5). **b** The bronchi narrowed sharply, immediately posterior to the first bronchial semiring (B1); the inflection occurred at B2 (*arrow*). The inflection was not marked in stained specimens; a fresh specimen is shown in ventral aspect (adult male *U. lomvia* from Greenland). **c** Air passages changed sharply in size and shape beginning at the pessulus, when they narrowed laterally and lengthened dorsoventrally; the narrowest and longest lumen occurred at B2 (*dashed outline*)

(n = 69–74 for Common Murres and 48–54 for Thick-billed Murres; all $P < 001$). Mean values of left- and right-side structures are used hereafter.

M. sternotrachealis did not tend to insert asymmetrically on one side of the trachea: 36 Common Murres showed approximately symmetric insertion, 14 had insertion farther anterior on the right side, and 14 others had insertion farther anterior on the left side. Corresponding numbers for Thick-billed Murres were 26, 12, and 21.

Size differences between sexes, geographic regions, and species

Overall, adult male Atlantic Common Murres were larger than females (in MANOVAs based on head + bill length and bone lengths; Table 1). However, MANOVAs were not significant when head + bill length was excluded, and only limb-bone lengths were used in the analysis (for Common Murres and Thick-billed Murres, respectively: Wilks's lambda = 0.746, $df = (6, 44)$, $F = 1.156$, $P = 0.35$; and Wilks's lambda = 0.752, $df = (6, 56)$, $F = 1.432$, $P = 0.22$). Furthermore, bone lengths did not differ between the sexes (Table 1). Syringeal size likewise did not differ between the sexes for either species in any geographic region (Table 2). With sexes combined, syringes in Pacific samples were larger within each species. Finally, Thick-billed Murres had a larger syrinx than Common Murres, but syringeal muscles did not differ in size (Table 2).

Measurements and size-scaling

General linear models with syringeal variables as response variables, and body-size variables as independent variables, revealed no differences between sexes in slope or intercept for adult Atlantic Common Murres or Atlantic–Arctic Thick-billed Murres (results of statistical tests not shown); therefore, based on these results and those reported above, we combined sexes within species for further analyses.

Within species, positive inter-correlations were found for all body-size variables (range of r, 0.3–0.8; all $P < 0.05$), and for all syringeal variables except muscle thickness in Thick-billed Murre (range of r, 0.2–0.5; all $P < 0.05$).

Various dimensions of the syrinx and syringeal muscles were correlated positively with body size (Fig. 3), hence expressed significant allometry, but no negative or positive allometry was found. Allometrically, four syringeal variables increased isometrically with body size: syringeal depth with head + bill length in Thick-billed Murres (slope ± 95% CI: 0.82 ± 0.61); syringeal width with length of humerus in Thick-billed Murres (slope ± 95% CI: 1.33 ± 1.02); and size of *M. sternotrachealis* with length of tarsometatarsus, in both species (slopes ± 95% CI: 1.85 ± 1.85 (Common Murre) and 1.90 ± 1.36 [Thick-billed Murre]).

Body-size-corrected comparisons of syringeal variables revealed that Thick-billed Murres had relatively larger syringes and larger *M. sternotrachealis*; *M. tracheolateralis* did not differ between species.

Discussion

General anatomy of the murre syrinx

The murre syrinx comprises several fused and calcified tracheal rings, plus first bronchial semirings. The tympanum is slightly more calcified in Common Murres. Calcification likely increases with age, at least up to 1 year of age, as it was less marked in a few juvenile specimens that we examined and was variable in older birds. Tracheal and syringeal calcification with age may be common in birds, but is poorly documented (Fitzgerald 1969; Hogg 1982; McLelland 1989). Other workers have noted that the tympanum is formed from tracheal rings, but the number of

Table 1 Summary of descriptive statistics on lengths of head + bill and fresh limb bones of Atlantic (Newfoundland) Common (*Uria aalge*) and Atlantic (Newfoundland)–Arctic (Coats Island, Nunavut; Nuuk, Greenland) Thick-billed (*U. lomvia*) Murre specimens used in the study

Sub-sample details	Body-size variable (lengths)			
	Head + bill[a]	Humerus[b]	Femur[b]	Tarsometatarsus[b]
Common Murre				
Adult female (n = 17)	107 ± 1[c]	87.0 ± 0.9	48.4 ± 0.8	39.2 ± 1.0
Adult male (n = 9)	109 ± 2	87.7 ± 0.8	49.3 ± 1.2	39.7 ± 1.2
Thick-billed Murre				
Adult female (n = 15)	100 ± 3[d]	89.8 ± 2.2	47.6 ± 1.3	37.5 ± 1.0[e]
Adult male (n = 16)	103 ± 2	90.3 ± 1.4	48.4 ± 1.1	38.4 ± 1.0

Cell entries are mean ± SD (mm). By MANOVA, males were the larger sex only in Common Murres (Wilks's lambda = 0.418, df = (8, 38), F = 2.595, P = 0.02; for Thick-billed Murres, Wilks's lambda = 0.642, df = (8, 50), F = 1.553, P = 0.16). Based on one-way ANOVAs, only head + bill length was larger in males (compared with Bonferroni-corrected α = 0.0125): Common Murres, df = (1, 22), F = 17.2, $P < 0.001$; Thick-billed Murre, df = (1, 28), F = 8.62, P = 0.007 (for Thick-billed Murres, length of tarsometatarsus, df = (1, 30), F = 6.84, P = 0.0126)

[a] Modified (see text)

[b] Measurements [mean ± SD (n)] by Spring (1971) on dried bones of common and Thick-billed Murres (respectively) were: humerus, 87.7 ± 2.0 (42) and 90.0 ± 2.2 (30); femur, 48.6 ± 1.3 (42) and 47.8 ± 1.8 (30); and tarsometatarsus, 38.8 ± 2.7 (40) and 37.1 ± 1.4 (30)

[c] n = 15

[d] n = 14 (excludes one unusually large measurement = 122 mm)

[e] n = 16

rings and the nature of their fusion have been confusingly described (Beddard 1898; King 1989; Warner 1969). King (1989, Fig. 3.32) incorrectly illustrated *Cartt. tracheosyringeales* and the pessulus as being completely fused with one another dorsally (compare our Fig. 1b).

The first bronchial semiring is very large and expanded anteriorly, especially around where *M. tracheolateralis* inserts, and is usually calcified beneath that muscle's insertion. This semiring is posterolateral to the tympanum, but is mobile and can move anteriorly to lie lateral to the tympanum, an action that presumably is effected by contraction of *M. tracheolateralis* during vocalization. Warner (1969, p 173) noted that the first bronchial semiring of murres was "significantly modified", but Beddard (1898, p. 363) incorrectly stated (and illustrated in his Fig. 176) that it "hardly differs from those that follow". Beddard (1898) and Warner (1969) observed that *M. tracheolateralis* inserts on the first bronchial semiring, whereas King (1989, p 153) incorrectly stated (and illustrated in his Fig. 3.32) that insertion is on "the most caudal part of the tympanum". Insertion of this muscle on one or more of the anterior bronchial semirings is a primitive state, and occurs throughout Alcidae (Gadow and Selenka 1891; Gadow 1896).

We confirmed the presence of only one potentially vibratile membrane, *Mem. tympaniformis medialis* (Warner 1969; King 1989). Warner (1969) noted elastin and collagen fibers in this membrane, and King (1989, p. 143) described its anterior "thickened…pad-like area". We also were struck by this thickening, which stained strongly due to the presence of cartilage (Fig. 1b, d). The thickened part of the membrane occurs where the bronchial lumen narrows sharply. We cannot suggest a functional explanation for these features, but similarly sharp narrowing of the lumen at the level of the second bronchial semiring also occurs in other alcids (unpublished observation).

The trachea is cartilaginous and collapsible in murres, yet completely calcified in eiders. Tracheal collapsibility may be an adaptation for deep diving (to ~200 m in murres vs ~20 m in eiders: Piatt and Nettleship 1985; Croll et al. 1992; Miller et al. 2007).

We found weak bilateral asymmetry in muscle size, with the right side being slightly larger in two of four comparisons. Bilateral asymmetry in vocal muscles, and in syringeal and bronchial skeletons, has been reported for many non-passerines, and the right side is larger in many; however, no phylogenetic or functional patterns are evident (Burke et al. 2007; Miller et al. 2007).

Sexual and species differences in the vocal tract

Vocal-tract size did not differ between the sexes in murres. Many published reports of sexual differences in the size of vocal structures may just reflect overall body-size differences between the sexes (Miller et al. 2007). Anecdotal evidence suggests some links between sexual differences in vocal-tract size and vocalizations. For example, males are smaller than females in Strigidae, but have a relatively larger syrinx and deeper voice. As noted, male Jungle Crows have longer tracheae, which may explain the lower-frequency formants in their calls (Tsukahara et al. 2006). In the Eurasian Collared Dove (*Streptopelia decaocto*), the

Table 2 Summary of descriptive statistics on syringeal measurements of Common (*Uria aalge*) and Thick-billed (*U. lomvia*) Murre specimens used in the study

Sub-sample details	Syringeal variable			
	Syr. breadth	Syr. depth[a]	*M. tracheolateralis*[a]	*M. sternotrachealis*[a]
Common Murre				
Atlantic: adult females ($n = 17$)	8.31 ± 0.42	8.51 ± 0.41	2.21 ± 0.22	2.18 ± 0.27
Atlantic: adult males ($n = 9$)	8.32 ± 0.29	8.53 ± 0.42	2.17 ± 0.16	2.28 ± 0.29
Atlantic: all adults ($n = 27$)	8.27 ± 0.41	8.52 ± 0.40	2.20 ± 0.20	2.22 ± 0.27
Atlantic: all juveniles ($n = 4$)	8.52 ± 0.24	8.70 ± 0.63	2.11 ± 0.19	1.84 ± 0.18
Pacific: adult females ($n = 10$)	9.29 ± 0.55	8.74 ± 0.46	2.36 ± 0.29	2.50 ± 0.39
Pacific: adult males ($n = 11$)	8.79 ± 0.50	8.68 ± 0.46	2.51 ± 0.33	2.37 ± 0.39
Pacific: all adults ($n = 21$)	9.03 ± 0.57	8.71 ± 0.45	2.44 ± 0.31	2.43 ± 0.38
Pacific: all juveniles ($n = 4$)	8.09 ± 0.73[b]	7.39 ± 1.24	1.83 ± 0.37	1.48 ± 0.40
Thick-billed Murre				
Atlantic–Arctic: adult females ($n = 15$)	8.74 ± 0.70	8.70 ± 0.54	2.21 ± 0.24	2.35 ± 0.28
Atlantic–Arctic: adult males ($n = 20$)	8.87 ± 0.40	8.64 ± 0.54	2.23 ± 0.33	2.36 ± 0.28
Atlantic–Arctic: all adults ($n = 39$)	8.84 ± 0.55	8.66 ± 0.51	2.23 ± 0.31	2.33 ± 0.32
Atlantic–Arctic: all juveniles ($n = 7$)	8.84 ± 0.45	8.86 ± 0.48	2.17 ± 0.20	2.16 ± 0.29
Pacific: adult females ($n = 7$)	9.86 ± 0.67	9.29 ± 0.55	2.44 ± 0.40	2.64 ± 0.38[c]
Pacific: adult males ($n = 9$)	9.49 ± 0.49	9.44 ± 0.58	2.71 ± 0.32	2.63 ± 0.52
Pacific: all adults ($n = 17$)	9.55 ± 0.70	9.31 ± 0.61	2.55 ± 0.40	2.61 ± 0.45[d]
Pacfic: all juveniles ($n = 1$)	8.90	8.00		

Cell entries are mean ± SD (mm). By MANOVA, adult males and females did not differ within geographic samples: Atlantic Common Murres (Wilks's lambda = 0.678, $df = (8, 42)$, $F = 1.125$, $P = 0.37$); Pacific Common Murres (Wilks's lambda = 0.749, $df = (4, 16)$, $F = 1.338$, $P = 0.30$); Atlantic–Arctic Thick-billed Murres (Wilks's lambda = 0.904, $df = (8, 66)$, $F = 0.427$, $P = 0.90$); and Pacific Thick-billed Murres (Wilks's lambda = 0.279, $df = (8, 20)$, $F = 2.229$, $P = 0.07$). Based on one-way ANOVAs (using Bonferroni-corrected $\alpha = 0.0125$), males and females did not differ in any variables. Adult syringes were larger in Pacific samples of each species: Common Murres (Wilks's lambda = 0.478, $df = (4, 43)$, $F = 11.7$, $P < 0.005$); and Thick-billed Murres (Wilks's lambda = 0.626, $df = (4, 50)$, $F = 7.48$, $P < 0.005$). Based on one-way ANOVAs (using Bonferroni-corrected $\alpha = 0.0125$), geographic samples within species differed in most variables: Common Murres (syringeal width: $df = (1, 49)$, $F = 24.8$, $P < 0.005$); Thick-billed Murres (syringeal width: $df = (1, 49)$, $F = 24.9$, $P < 0.005$; syringeal depth: $df = (1, 49)$, $F = 19.2$, $P < 0.005$; *M. tracheolateralis*: $df = (1, 49)$, $F = 15.2$, $P < 0.005$; *M. sternotrachealis*: $df = (1, 48)$, $F = 7.49$, $P = 0.009$). Adult Thick-billed Murres had larger syringes (Wilks's lambda = 0.875, $df = (4, 98)$, $F = 3.50$, $P < 0.005$). Based on one-way ANOVAs (using Bonferroni-corrected $\alpha = 0.0125$), adults differed between species in syringeal but not muscle size (syringeal width: $df = (1, 97)$, $F = 13.2$, $P < 0.005$; syringeal depth: $df = (1, 98)$, $F = 9.04$, $P = 0.003$)

[a] Means of left and right sides for each specimen (measurements on fluid-preserved specimens were adjusted for shrinkage; see text)

[b] $n = 3$

[c] $n = 6$

[d] $n = 16$

male's trachea is longer, vocal muscles and the syringeal skeleton are larger, etc., and male calls have a lower fundamental frequency (Ballintijn and Ten Cate 1997). Sexual differences in murre vocalizations have not been investigated.

The syrinx and *M. sternotrachealis* were larger in Thick-billed Murre. However, the trachea is ~10% longer in Common Murres, in keeping with overall body-form differences between the species: Thick-billed Murres are stockier and have a shorter neck (Spring 1971). A difference of that magnitude in tracheal length should result in different filtering effects on vocalizations of the species. A comparative study of murre vocalizations is needed to investigate vocal correlates of these size differences.

To our knowledge, the only previous allometric analysis of vocal-tract size is our study on a sexually-selected trait (size of the tracheal bulla) in two eider species (Miller et al. 2007). In that study, most allometric regressions were significant and positive. In the present study, few allometric regressions of syringeal- on body-size variables within species were significant, and all exhibited isometry; no positive allometry was detected. This is not surprising, because allometry is usually more marked when it involves sexually-selected characters or interspecific comparisons (Rensch 1959; Cock 1966). In summary, fewer allometric relationships were found and allometric patterns were weaker in murres than in eiders, although the significant relationship of size (width) of *M. sternotrachealis* to

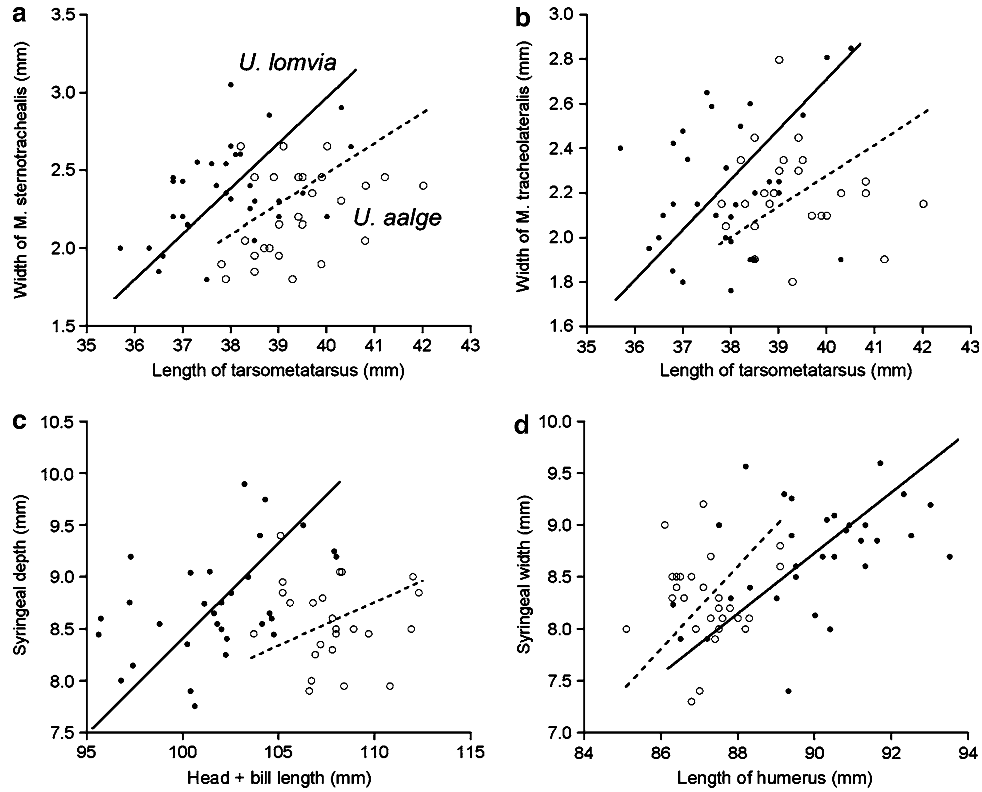

Fig. 3 Examples of bivariate relationships for syringeal-size to body-size variables in murres (*Uria*). Regression lines from reduced major axis regression are included only as visual guides. Relationships that exhibited significant allometry were: syringeal depth in relation to head + bill length, and syringeal width in relation to length of humerus, in *U. lomvia*; and with of *M. sternotrachealis* to length of tarsometatarsus, in both *U. aalge* and *U. lomvia* (see text)

tarsometatarsal length in both murre species stands out. Interpretation of this finding requires research on both functional and broader phylogenetic scales.

Qualitatively, the vocal tract is very similar between the two murre species. Vocalizations and vocal repertoires of other alcids are far more complex than those of murres (Seneviratne et al., unpublished), so the morphological and quantitative description we have provided can serve as a basis for broader comparative studies within the family.

Zusammenfassung

Syrinxanatomie und -allometrie bei Lummen (Alcidae: *Uria*)

Art- und Geschlechtsunterschiede in Lautgebung und Lautbildungstrakt sind weit verbreitet. Wir haben den Lautbildungstrakt von Trottellummen (*Uria aalge*) und Dickschnabellummen (*U. lomvia*) untersucht. Wir hatten anatomische oder allometrische Unterschiede bei Altvögeln zwischen Arten und Geschlechtern vorausgesagt, aufgrund von Unterschieden, die mit dem Sozialverhalten zusammenhängen (Trottellummen nisten in höheren Dichten, Männchen sind das aggressivere Geschlecht etc.). Der Lautbildungstrakt war anatomisch einfach aufgebaut und ähnlich zwischen Arten und Geschlechtern. Die Luftröhre bestand hauptsächlich aus Knorpel, doch die am weitesten hinten liegenden 4–6 Ringe waren verkalkt und als Teil der Syrinx zum Tympanum verschmolzen. Die Syrinx schloss die (nicht verschmolzenen) ersten bronchialen Halbringe ein, die unterhalb der Ansatzstelle des Musculus tracheolateralis vergrößert und verkalkt waren. Eine schwache bilaterale Asymmetrie (größere rechte Seite) trat jeweils in der Breite des *M. tracheolateralis* und des *M. sternotrachealis* auf. Die Luftröhre war bei Trottellummen etwa 10% länger; das Tympanum und die Breite des *M. sternotrachealis* waren bei Dickschnabellummen relativ größer. Lautbildungstraktmorphologie und -größe unterschieden sich bei beiden Arten nicht zwischen den Geschlechtern. Allometrische Analysen von Altvögeln zeigten Isometrie in a) Tympanumgröße im Verhältnis zu Kopf- + Schnabellänge bzw. Humeruslänge bei Dickschnabellummen und b) Breite des *M. sternotrachealis* im Verhältnis zur Tarsometatarsuslänge bei beiden Arten. Vergleichende Feldstudien von Arten und Geschlechtern sind notwendig, um die funktionale Bedeutung unserer Befunde in Bezug auf Lautgebung zu klären.

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