

Patterns of vocal divergence in a group of non-oscine birds (auklets; Alcidae, Charadriiformes)

Sampath S. Seneviratne^{1,2}, Ian L. Jones¹ and Steven M. Carr¹

¹Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada and

²Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada

ABSTRACT

Question: Are phylogenetic relationships the major determinant of vocal relationships in non-oscine birds (birds that do not have a learning component in the vocalization)?

Background: Both environmental variables and phylogenetic affinities can affect vocalizations. Unlearned vocalizations are characteristics of most non-oscine bird families, which have a relatively less-complex syrinx and vocalizations.

Organism: A monophyletic group of underground-nesting seabirds (auklets: Aethiini, Alcidae, Charadriiformes) from the Aleutian Islands, Alaska, USA.

Methods: We mapped vocal characters (28 acoustic and 10 syringeal) from total repertoires of all members of the tribe Aethiini onto a molecular phylogeny to compare the relative influence of phylogeny and breeding habitat on vocal divergence.

Conclusion: Phylogeny, visual display, and ecological factors have contributed to vocal divergence in this clade. Temporal attributes and syringeal attributes of the acoustics of vocalization showed high congruence with phylogeny. Frequency attributes, which are affected by environmental variables, showed low congruence, and therefore high homoplasy.

Keywords: Alcidae, auklets, character reconstruction, display evolution, non-oscine birds, phylogeny, vocalization.

INTRODUCTION

Vocalizations are sensitive indicators of speciation and population divergence (Lanyon, 1969; Payne, 1986; Martens, 1996; Price and Lanyon, 2002; Isler *et al.*, 2007; Miller and Baker, 2009), and are used routinely in modern species-level systematics (Cuervo *et al.*, 2005; Athreya, 2006; Alström *et al.*, 2007). Vocal behaviour has also been studied to elucidate the phylogenetic history of species groups (e.g. Irwin, 1996; Price and Lanyon, 2002). In birds, vocalizations that are not learned are likely to be especially informative phylogenetically (Miller and Baker, 2009). Such vocalizations are widespread in non-oscine birds (whose vocalizations do not have a learned component), and are characteristic of most bird groups [27 of 30 orders, excluding Passeriformes,

Correspondence: S.S. Seneviratne, Biodiversity Research Centre, University of British Columbia, 6270 University Blvd., Vancouver, BC V6T 1Z4, Canada. e-mail: sampath@zoology.ubc.ca

Consult the copyright statement on the inside front cover for non-commercial copying policies.

Psittaciformes, and Apodiformes (Nottebohm, 1972; Baptista and Schuchmann, 1990; Bradbury and Vehrencamp, 1998; Jarvis, 2006)].

Vocal learning is a main driver of speciation in birds, generating pre-zygotic isolation through local dialects (Baptista and Trail, 1992; Edwards *et al.*, 2005). For example, order Passeriformes (songbirds), which includes the oscines (suborder Passere, which has a complex syrinx) and the sub-oscines (suborder Tyranni), represents about half of all known bird species. In the absence of vocal learning, non-oscine birds might have a slower rate of vocal divergence and a higher phylogenetic component to the vocalization signal. Conversely, certain aspects of oscine vocal displays are also evolutionarily conservative (Kroodsma and Candy, 1985; Payne, 1986; Baptista and Trail, 1992; Irwin, 2000; Päckert *et al.*, 2003). Thus, vocal properties have a genetic basis, and vocal similarities between species may depend on their phylogenetic relatedness (Catchpole, 1980; Kroodsma and Candy, 1985; Payne, 1986; Price and Lanyon, 2002; Päckert *et al.*, 2003; Miller and Baker, 2009).

The physical environment shapes the properties of vocal signals (McCracken and Sheldon, 1997) and similarities may result from convergence (Seddon, 2005; Nicholls and Goldizen, 2006). Calls of distantly related species that live in similar habitats may be more similar than calls of closely related species that live in different habitats (Endler, 1993; Badyaev and Leaf, 1997; Tobias *et al.*, 2010). Properties of vocal signals vary with their signalling context as well, resulting in homoplasy in vocal traits that serve specific functions in specific acoustic environments (Marler, 1955). Similarly, the influence of morphology such as the beak (Podos and Nowicki, 2004) and body size (Bertelli and Tubaro, 2002) can contribute to vocal divergence in birds. Irwin (2000) showed that stochastic changes alone could lead to vocal divergence. As a result of the mechanical origin of the vocal signal, certain sound properties can be linked with the physical properties of the syrinx (Bertelli and Tubaro, 2002).

Several studies have compared vocal divergence in sub-oscines (e.g. antbirds) or non-oscines (e.g. pigeons and doves). These comparative studies, however, used a single or a few selected display types for comparison across individuals or lineages. For example, Slabbekoorn *et al.* (1999) and Kort and ten Cate (2004) studied the phylogenetic affinities of the ‘coo’ songs of doves. Seddon (2005) looked at song as a species-recognition device in antbirds. Use of one or a few types of vocal display (mostly the most prominent song) is useful to elucidate the phylogenetic history but does not explore the divergence of the vocal repertoire. On the other hand, comparative analysis of diverse sets of sound classes should be more informative in elucidating the evolutionary processes of vocal divergence in groups with complex vocalizations and large repertoires (Catchpole, 1982; Irwin, 1996; Isler *et al.*, 2007). We undertook such a study for a tribe of five species of underground-nesting seabirds – the auklets (tribe Aethiini, family Alcidae, order Charadriiformes). We used comparable information on the complete vocal repertoires of each species.

In Alcidae, the tribe Aethiini is a monophyletic lineage (Paton *et al.*, 2003; Thomas *et al.*, 2004; Paton and Baker, 2006; Pereira and Baker, 2008; Humphries and Winker, 2010) (Fig. 1). Cassin’s auklet (*Ptychorhamphus aleuticus*) is the sister species to the remaining four species of *Aethia* (Strauch, 1985; Moum *et al.*, 1994; Friesen *et al.*, 1996; Thomas *et al.*, 2004; Pereira and Baker, 2008; Humphries and Winker, 2010). Auklets are highly vocal at the breeding colony (Seneviratne *et al.*, 2009). Most species attend their colony during daytime, whereas *Ptychorhamphus* and whiskered auklets (*Aethia pygmaea*) visit their colonies only at night (Gaston and Jones, 1998). Breeding habitats vary:

- *Ptychorhamphus* breeds in soft soil in slopes covered with grass or trees (Thoresen, 1964; Manuwal and Thoresen, 1993);

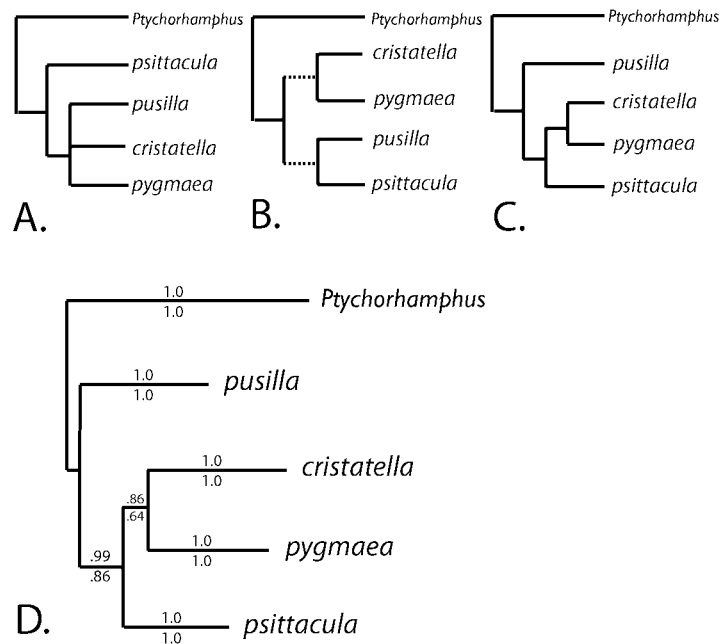


Fig. 1. Phylogenetic relationships of the Aethiini based on (A) morphology (Strauch, 1985), (B) mitochondrial DNA and allozymes (Friesen *et al.*, 1996), (C) mitochondrial and nuclear DNA (Pereira and Baker, 2008), and (D) mitochondrial DNA [ND2 (Humphries and Winker, 2010)]. The numbers on branches represent posterior probability values for two models of evolution, and broken lines indicate less defined branches.

- crested auklets (*A. cristatella*) and least auklets (*A. pusilla*) breed in rock crevices (Jones, 1993a, 1993b);
- *Aethia pygmaea* breeds in rock crevices, and soil and grassy slopes embedded within rocks (Zubakin and Konyukhov, 1999; Hunter *et al.*, 2002);
- parakeet auklets (*A. psittacula*) breed in rock crevices, natural cavities in soil, and self-excavated burrows (Jones *et al.*, 2001).

Here, we use both acoustic characters from total repertoires and syringeal characters (which, together, we call ‘vocal characters’) to identify correlates with vocal divergence.

We test three competing hypotheses:

Hypothesis 1: Since Aethiini comprises a group of non-oscine birds, phylogenetic relationships largely determine vocal evolution in auklets.

Prediction: The vocalization of the sister pair *cristatella* and *pygmaea* is more similar to each other than those of *pusilla*, *psittacula*, and *Ptychorhamphus*.

Hypothesis 2: If vocalization reflects adaptations to the breeding habitat, then vocal divergence should reflect the divergence of breeding habitats.

Prediction: Crevice-dwelling auklets share a set of similar vocal display characters and grassland nesters share a different set.

Hypothesis 3: The complexity of visual ornamentation reduces the (sexual) selection pressure on the vocal display, reducing the complexity of vocalization.

Prediction: Since the complexity of the visual display increases along the phylogenetic tree in Aethiini, the vocal complexity diminishes along the tree.

The molecular phylogeny adopted here uses genetic markers that we assume are neutral with respect to the vocal traits that we compared (Humphries and Winker, 2010) (Fig. 1). Those neutral markers give us phylogenetic relationships that do not have a direct influence on the traits that we examined or the parameters that we compared. We test whether the vocal traits correlate with the phylogenetic relationships. If so, then the traits in question follow parameters similar to that of molecular phylogeny – and the habitat parameters do not contribute to the explanation.

METHODS

Study sites and display recordings

Vocal recordings were made at Buldir Island (52°22'N, 175°54'E) and Egg Island (53°52'N, 166°03'W), Aleutian Islands, Alaska, during times of peak colony attendance of each species. Both islands are talus- and grass-covered, treeless volcanic islands with large breeding colonies of auklets (Byrd and Day, 1986; Bradstreet and Herter, 1990). We recorded vocalizations with a Sony TCD-D10PROII Digital Audio Tape recorder (sampling rates 32, 44.1, and 44.2 kHz) or Fostex FR-2 solid-state recorder (sampling rate 48.1 kHz), with Sennheiser MKH 70 or MKH 816 directional microphones. Our recording sessions totalled ~80 hours. We used Raven 1.2.1 (Bioacoustics Program, Cornell Lab of Ornithology, New York) to characterize the vocal repertoire using a combination of audible differences on spectrograms (Hailman and Ficken, 1996; Marler and Slabbekoorn, 2004; Seddon, 2005) and explicit measurements of physical properties. We referred to different kinds of basic sound elements (the shortest sound sections in the spectrogram isolated from sections of silence) as 'notes' following Marler and Pickert (1984), Marler and Slabbekoorn (2004), and Seneviratne *et al.* (2009). Acoustic measurements included:

- Duration
- Frequency
- Modulation of the carrier frequency
- Harmonic structure
- F, Frequency: F_n , frequency of n th harmonic; F_0 , fundamental frequency; F_μ , frequency of the harmonic that has the highest intensity in the power spectrum; CF_n , carrier frequency of n th harmonic; FM, frequency modulation (for methods and analysis, see Seneviratne *et al.*, 2009).

Selection and scoring of acoustic characters

Following Miller (1996), McCracken and Sheldon (1997), and Price and Lanyon (2002), we hypothesized 28 probable homologies from the repertoires above. Continuous characters were assigned to discrete categories (character states 0, 1, and 2) by the method of Price and Lanyon (2002). For each continuous character, we determined 95% confidence intervals from

three representative individuals, and considered the non-overlapping regions of character distribution as a character state. Continuous characters that could not be subdivided by this method were excluded from the analysis. Other characters were characterized as ‘present’ or ‘absent’. Character states that represent *Ptychorhamphus* were assigned the ‘0’ state except when it represented the middle state of three non-overlapping states (‘1’). Auklets are sexually monomorphic, thus we were unable to assign acoustic characters to a sex.

Selection and scoring of syringeal characters

Sound production differences may be directly linked with the structural differences of the syrinx (King, 1989; Baptista and Trail, 1992). Therefore, syringeal characters might reflect phylogenetic affinities. Following Cannell (1988), the syrinx (the vocal tract up to mid-trachea and proximal parts of the bronchi) was removed from fresh specimens of all species of *Aethia* from Buldir Island and stored in 70% ethanol. Three specimens from each species were used for the measurements. Because of the limited specimens available, we used syrinxes of both sexes (no information is available on sexual dimorphism in auklet syrinxes). We measured the preserved syrinx and syringeal muscles under a dissecting microscope with an ocular micrometer (calibrated with a stage micrometer) with 10× magnification. The following variables were measured (± 0.1 mm):

- dorsoventral depth of the syrinx, on left and right sides;
- breadth of the syrinx, from the dorsal aspect;
- maximal diameter of the m. tracheolateralis and m. sternotrachealis on left and right sides (see Table 1).

After measurements, we stained vocal tracts for cartilage and calcium phosphates with Alcian blue and Alizarin red, and then stored them in 90% glycerin (Cannell, 1988). Using the same microscope set-up, we qualitatively measured the amount of calcification in the syringeal rings, bronchial semirings and pessulus, and amount of ring fusion in calcified rings on stained specimens (see Table 1). Correlation of syringeal size with body mass was determined with JMP 7.0 (SAS Institute Inc., Cary, NC). Data for mean body mass were taken from Jones (1993a, 1993b) and Gaston and Jones (1998).

Reconstruction of character changes

Using the program PAUP 4.10b (Swofford, 2002) with the exhaustive search option, we estimated the most parsimonious vocal (acoustic and syringeal) phylograms. All 38 characters were assigned equal weight. We mapped vocal characters (see Appendix) onto the most recent molecular phylogeny proposed by Pereira and Baker (2008) and Humphries and Winker (2010) (Fig. 1D) with PAUP (with MulTrees option). We calculated the consistency index, CI (Kluge and Farris, 1969) and retention index, RI (Farris, 1989) of each character to evaluate overall congruence between the molecular tree and the vocal phylogeny (Burns, 1998; Omland and Lanyon, 2000; Price and Lanyon, 2002). Simple parsimony with delayed character transformation (DELTRAN) was used to map and compare putative apomorphies (Maddison and Maddison, 1992). We used MacClade 3.5 (Maddison and Maddison, 1992) to estimate character changes based on molecular topology.

RESULTS

Vocal repertoire

The vocal repertoire of auklets is complex and large (22 total display types), and is characterized by 1–5 frequency modulated and harmonically rich note types (28 types across species) arranged sequentially in varied combinations (Seneviratne *et al.*, 2009). The characteristics of notes and their appearance in displays were intra-specifically consistent. We have identified two groups based on syntactical arrangement of note types (Fig. 2): (1) an alternate-element arrangement in *Ptychorhamphus* and *psittacula*; and (2) an arrangement of sequentially graded notes throughout the display in *pygmaea* and *pusilla*. The repertoire of *cristatella* was close to that of *pygmaea*, except that one display type showed an alternate arrangement of notes (Seneviratne *et al.*, 2009).

Syringeal anatomy

The structure and general appearance of syrinxes were similar among all auklet species, and were similar to other alcid syrinxes (Warner, 1969; Miller *et al.*, 2008). Tracheal rings were cartilaginous and separated from the elastic membrane. Rings were notched in dorsal and ventral median lines. The syrinx of *cristatella* was the largest, followed by those of *Ptychorhamphus*, *psittacula*, *pygmaea*, and *pusilla* (Table 1). Syringeal size (PC1 of syringeal width, mean depth, mean width of m. sternotrachialis and that of m. tracheolateralis) was positively correlated with average body weight ($F_{1,12} = 13.63$, $P = 0.003$, $R^2 = 0.53$). However, syringeal musculature varied little among species and did not reflect the pattern of variation present in syringeal dimensions across species (Table 1). Calcification of tracheal rings was limited to the posterior portion of the trachea. *Ptychorhamphus* had the greatest degree of calcification (~7 calcified rings). *Aethia* had ~5 calcified rings (Table 1).

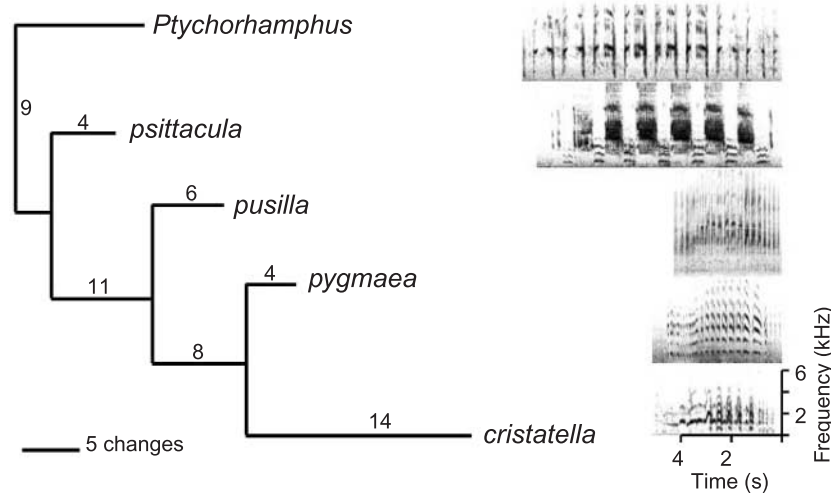


Fig. 2. Minimum length tree for the vocal (acoustic and syringeal) character matrix generated by simple parsimony. Numbers on each branch indicate number of character changes. A representative display type; advertisement display for each species is also shown.

Acoustic and syringeal (vocal) character matrix

The Appendix summarizes the 38 vocal characters used for the vocal phylogram. Characters 1–10 (basic sound envelopes) and 18–20 represent the structural information of auklet acoustics, and the complexity and sound production capacity of the syrinx. Characters 11–28 represent temporal variation of the display, and characters 29–38 describe syringeal anatomy. Characters 1, 5, 7, 11, 14, and 16–38 each had two alternative character states (0, 1), and each of the others had three non-overlapping states (0–2). Of the 38 characters used (see Appendix and Table 2), 19 were parsimony-informative. The shortest tree obtained from simple parsimony required 56 character changes. In the rooted tree (Fig. 2), *psittacula* was basal to *Aethia*, and *cristatella* and *pygmaea* were placed as a sister group. The length of the remaining trees varied from 57 to 66.

Reconstruction of vocal character change

Disagreement between the vocal characters and molecular phylogeny was evident from the low CI and RI values (Table 3). The overall CI and RI value was 0.76 and 0.33 respectively. The temporal and syringeal characters had a higher CI and RI (Table 3), but frequency-related characters showed a lower CI and RI (Table 3). Only 25% of the temporal and 10% of the syringeal characters had low CI values, whereas 58% of frequency-related characters had low CI (Table 4).

The smaller number of character changes in some branches and among nodes (Fig. 3) further reflects a poor fit between trees. About 30% of character changes are concentrated at the branch leading to *A. pusilla*, but only 2% of the changes found in the node separated the rest of the *Aethia* from *pusilla* (Fig. 3). When *pusilla* was removed from the analysis, the topology of the tree matched the molecular phylogeny (CI = 0.98, RI = 0.91). Similarly, in the absence of *psittacula*, the overall CI and RI value increased to 0.86 and 0.50 respectively (Table 3). Therefore, the position of either *pusilla* or *psittacula* constitutes the difference between the vocal and molecular trees.

DISCUSSION

The Aethiini auklets have undergone a striking diversification of visual displays, yet the pattern of their vocal display diversity remains enigmatic. We have sought to elucidate some of the evolutionary forces that determine vocal diversity in these highly vocal, burrow-nesting seabirds to understand patterns of divergence in non-oscine vocalization. Overall, 11 characters (29%) showed evidence of character reversal, convergence or both. These include six frequency-related characters (50%), four temporal characters (25%), and one syringeal character (10%). The lower overall CI and RI values that we observed in vocal traits (CI = 0.76 and RI = 0.33) indicate higher homoplasy, especially in the frequency-related characters. Therefore, the evolution of acoustic display and vocal apparatus has not proceeded in a completely parsimonious manner with the molecular phylogeny in Aethiini (Table 3). However, both temporal and syringeal characters reflected a lower homoplasy.

We used the anatomy of the sound production organ, the complete vocal repertoire of the clade, and the acoustic properties of the habitat to test the patterns of vocal diversity. To our knowledge, just one other study used a large body of vocal information in

Table 1. Summary of descriptive statistics on syringeal characters of auklets (Aethiini)

Species	Mean dimensions (s.d.) (mm)					No. of calcified rings (range)				
	29	30	31	32	33	34	35	36	37	38
<i>Ptychorhamphus</i>	4.9 (0.7)	4.6 (0.3)	0.8 (0.0)	1.2 (0.1)	7 (6–7)	3 (0–3)	5 (4–5)	7 (6–7)	7 (3–7)	partial
<i>A. cristatella</i>	5.1 (0.1)	5.5 (0.1)	0.9 (0.0)	2.2 (0.0)	5 (4–5)	0 (0)	0 (0)	5 (4–5)	0 (0)	partial
<i>A. pusilla</i>	3.8 (0.1)	4.1 (0.2)	0.9 (0.0)	1.5 (0.0)	5 (4–5)	2 (2)	3 (3)	4 (4)	4 (2–4)	complete
<i>A. psittacula</i>	4.4 (0.3)	4.7 (0.3)	0.9 (0.1)	1.5 (0.2)	5 (4–5)	2 (0–2)	4 (3–4)	4 (4)	4 (0–4)	complete
<i>A. pygmaea</i>	3.9 (0.3)	4.0 (0.2)	0.9 (0.0)	1.4 (0.3)	5 (4–5)	1 (0–1)	5 (3–5)	5 (3–5)	3 (0–3)	partial

Note: The numbers in the header row indicate the character numbers in the Appendix.

Table 2. Character matrix for the vocal phylogram

Species	Character state																			
	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	1	1
<i>Ptychorhamphus</i>	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
<i>A. cristatella</i>	0	2	1	0	0	2	1	0	0	1	1	0	1	1	0	1	1	1	1	1
<i>A. pusilla</i>	0	0	0	2	2	0	1	1	2	0	1	1	0	1	0	1	1	1	0	0
<i>A. psittacula</i>	0	1	2	0	1	0	1	2	0	2	0	1	1	0	0	0	0	1	0	0
<i>A. pygmaea</i>	1	1	1	2	2	1	1	0	0	1	1	1	1	1	0	1	1	0	0	1

Note: Character numbers and states are as in the Appendix.

Table 3. Summary of character analysis for the different vocal attributes

	No. of characters	CI	RI
Total	38	0.76	0.33
Acoustic characters	28	0.73	0.24
temporal	16	0.82	0.33
frequency	12	0.65	0.18
Syringeal characters	10	0.91	0.75
Tree without <i>psittacula</i>	38 (4 taxa)	0.86	0.50
Tree without <i>pusilla</i>	38 (4 taxa)	0.98	0.91

Note: CI = consistency index, RI = retention index.

Table 4. Measures of homoplasy for vocal characters mapped on to the molecular phylogeny

Character	CI	Character	CI
Temporal characters			
1 Number of note types	1.0	7 F_0	1.0
2 Minimum note length	1.0	8 Largest number of peaks in a note	1.0
3 Maximum note length	1.0	9 Lowest range FM	1.0
11 Number of vocalization types	1.0	10 Highest range FM	0.7
13 Minimum length of vocalization	1.0	18 Pure tones	1.0
12 Maximum length of vocalization	1.0	19 Trills	0.5
14 Number of note types in a vocalization	1.0	20 Broadband noise	0.5
15 Minimum note spacing	0.5	21 FM in vocalization	1.0
16 Structural organization of vocalization	1.0	23 Sequentially graded note types	0.5
17 Pulse	1.0		
22 Alternate arrangement of note types	0.5	Syringeal characters	
24 Clustered arrangement of note types	0.5	29 Syringeal width	0.5
25 Formation of rafts	1.0	30 Mean syringeal depth	1.0
26 Aerial vocalization	1.0	31 Mean width of m. tracheolateralis	1.0
27 Synchronous vocalization	1.0	32 Mean width of m. sternotrachealis	1.0
28 Duet	0.5	33 Number of calcified rings	1.0
		34 Completely calcified rings	1.0
Frequency characters		35 Ventral syringeal calcification	1.0
4 Minimum F_μ	0.5	36 Dorsal syringeal calcification	1.0
5 Maximum F_μ	0.7	37 Fused syringeal rings	1.0
6 Harmonic level of F_μ	0.5	38 Calcification of pessulus	1.0

a comparative analysis that studied the phylogenetic signal (Price and Lanyon, 2002) – in Oropendolas, a group with vocal learning (oscine). Here, we assessed the phylogenetic and environmental factors that contribute to vocal divergence in a non-oscine bird group. Results of our study confirm McCracken and Sheldon's (1997) observations. We showed that divergent selection of social and ecological factors could act on vocal repertoires. Such forces could mask the phylogenetic signal even in non-oscines.

We compared vocal displays of each species in the group in relation to molecular phylogeny, an approach that has proven effective in elucidating evolutionary patterns (e.g. Burns, 1998; Slabbekoorn *et al.*, 1999; Price and Lanyon, 2002; Päckert *et al.*, 2003; Kort and ten Cate, 2004), although

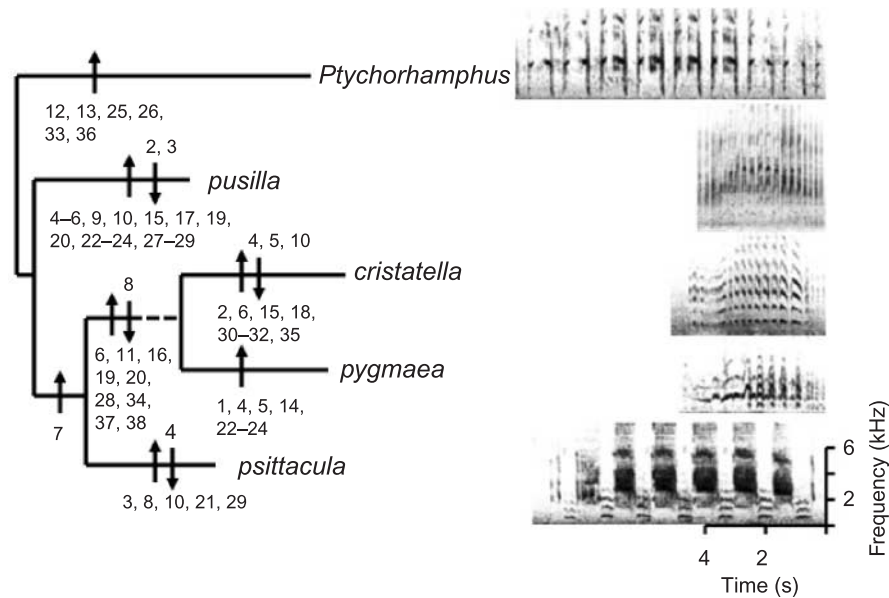


Fig. 3. Evolutionary changes of vocal characters reconstructed on the molecular phylogeny (Humphries and Winker, 2010) (Fig. 1D). Unambiguous character changes are shown as arrows along the branches (up arrows for gain/increase and down arrows for loss/decrease) with the character numbers as in the Appendix. Spectrograms of advertisement display are also aligned as in Fig. 2.

weaknesses have been outlined by Atz (1970), Frumhoff and Reeve (1994), Westoby *et al.* (1995), Price (1997), Cunningham *et al.* (1998), and Masters (2007). The CI is inversely proportional to the number of characters used for the analysis (Wimberger and Queiroz, 1996). Since our analysis encompassed a large number of characters, CI might have been expected to be smaller. However, RI, which does not correlate with the number of characters used (Price and Lanyon, 2002), reflected a similar pattern (Table 3).

The overall incongruence of two phylogenies is due to the placement of *pusilla* and *psittacula* (Figs. 2, 3). Despite the position of *psittacula* as the sister species to the *pygmaea* and *cristatella* pair in the molecular phylogeny (Fig. 1D), the arrangement of notes and some of the display types of *Ptychorhamphus* and *psittacula* are remarkably similar (Seneviratne *et al.*, 2009). For example, *Ptychorhamphus*'s *Kree-er* and *Kut-I-er* displays are acoustically similar to *psittacula*'s *Raft-whinny* and *Whinny* displays, respectively (Seneviratne *et al.*, 2009). They are, however, delivered in different contexts (Seneviratne *et al.*, 2009). *Aethia pusilla*'s repertoire consists of highly graded note types with rapid, frequency-modulated trills, which is closest to the repertoires of *pygmaea* (Seneviratne *et al.*, 2009). The highest number of character changes (31%) also took place at the branch leading to *pusilla*, causing conflict between the two phylogenies (Figs. 2, 3). This could be (a) vocal convergence of *pusilla* to the *pygmaea* and *cristatella* pair (as suggested in the molecular topography), (b) reversal of *psittacula* to the ancestral type (making its vocalization similar to that of *Ptychorhamphus*), or (c) a low resolution of the molecular phylogeny [caused by a polytomy (Walsh *et al.*, 1999; Seneviratne, 2009; Humphries and Winker, 2010)] that prevents capturing the true phylogenetic relationships.

Placement of *pygmaea* and *cristatella* as a sister pair in the molecular phylogeny agrees with the vocal relationships, which also supports our hypothesis (1) – that is, phylogenetic

relationships are a major determinant of vocal evolution in Aethiini. Vocal homologies were evident in the repertoire of this pair, which is characterized by sequential gradation of element complexity, the characteristics of carrier frequency (CF), and the lack of broadband noise. *Aethia cristatella*'s *Trumpet*, *Cackle*, and *Bark* displays are structurally and functionally analogous to *pygmaea*'s *Staccato Beedoo*, *Duet Beedoo*, and *Bark* displays respectively (Seneviratne *et al.*, 2009).

The importance of habitat for vocal diversification has been previously suggested. Open habitats transmit sounds better than densely vegetated habitats (Morton, 1975; Marten and Marler, 1977; Blumenrath and Dabelsteen, 2004; Nicholls and Goldizen, 2006). Natural selection favours signals with optimum signal transmission (Endler, 1992; Bradbury and Vehrencamp, 1998). Therefore, habitat characteristics such as vegetation cover, density, and the amount of reverberation from rocks and sound-absorptive loose soil should be able to alter both frequency (Wiley, 1991; Badyaev and Leaf, 1997; Bertelli and Tubaro, 2002) and temporal attributes of the vocal signal (Wiley, 1991; Nicholls and Goldizen, 2006). In auklet vocalization, temporal attributes do not appear to be related to habitat, whereas frequency attributes appear to be (see also McCracken and Sheldon, 1997). Such habitat-enforced selection could partly explain the similarity observed between the vocal repertoires of *Ptychorhamphus* and *psittacula* (Fig. 4B), supporting our hypothesis (2) that vocal divergence reflects the divergence of breeding habitats. Both species had higher frequency (F_{μ} ; see Methods), which might be selected for close-to-ground vocal display (Marten and Marler, 1977; Marten *et al.*, 1977), because both breed in grassy slopes with soft soil and vocalize in front of the burrow (see Introduction). Vocally similar *pusilla*, *pygmaea*, and *cristatella* breed in talus slopes (see Introduction). These three species vocalize in the rafts, from the boulders, and inside the rocky crevices (Gaston and Jones, 1998; Seneviratne *et al.*, 2009).

Facial ornamentation (visual display) differences are congruent with molecular phylogeny in Aethiini (Jones, 1999; Pereira and Baker, 2008; Humphries and Winker, 2010). *Ptychorhamphus*, with the least ornamentation, is the outgroup to more ornate *Aethia*, and the similar patterns of *cristatella* and *pygmaea* are the most recently evolved. The unique feather odour (Hagelin and Jones, 2007), forward curving long crest, dark throat, belly, and elongated facial feathers are shared by these most recent species of *Aethia*. *Aethia pusilla* and *psittacula* are similar in appearance; they have a pale belly and throat, and similar body proportions (Jones, 1999). Their vocal characteristics follow this same pattern of visual and chemical display (Fig. 4A). However, contrary to our hypothesis (3) that complexity of visual ornamentation reduces the complexity of vocalization, we noticed no reduction or gain in complexity in vocalization along the tree.

Elaborate visual display in *Aethia* is a product of both sexual and natural selection (Jones and Hunter, 1993; Jones, 1999; Seneviratne and Jones, 2008, 2010). These same selection forces that have acted on ornamental traits could have acted on vocal traits and led to the observed parallel patterns (Fig. 4A). Sexually selected displays can evolve rapidly, thus they are sensitive indicators of low-level divergence (Kaneshiro, 1988; Uy and Borgia, 2000). However, homoplasy would prevail when the options for change are limited (Atz, 1970; Masters, 2007). In such circumstances, behaviours that are subjected to sexual selection might suffer a higher level of homoplasy (Omland and Lanyon, 2000; Masters, 2007), which, in turn, might partly explain our lower CI values.

The nocturnal colony attendance behaviour of colonial seabirds can affect vocal divergence (Park *et al.*, 1940; Jones *et al.*, 1989a), and nocturnal alcids show greater complexity in their vocal repertoires than do diurnal alcids (Jones *et al.*, 1987, 1989b; Drost and Lewis, 1995; Nelson, 1997). However, we did not observe any difference in the complexity of repertoires of nocturnal

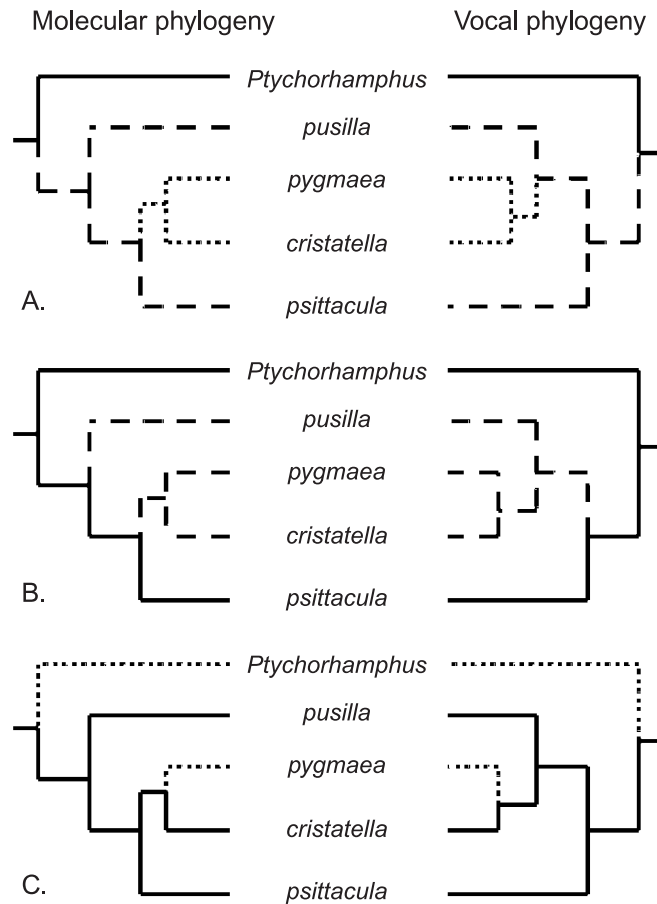


Fig. 4. Some speculations for vocal divergence in Aethiini: (A) the level of ornament expression – highly ornamented (dotted line), ornamented (broken line), and sparsely ornamented (solid line); (B) breeding habitat – vegetated soft soil (solid line) and rock crevices (broken line); (C) colony attendance behaviour – nocturnal (dotted line) and diurnal (solid line).

auklets from that of their diurnal congeners (Seneviratne *et al.*, 2009). Nor did we find a clear effect of colony attendance behaviour on vocal divergence (Fig. 4C).

Summary

The temporal and syringeal attributes of the vocal relationships agreed with phylogenetic affinities in auklets. The frequency attributes were less congruent with the molecular phylogeny but did reflect the divergence of breeding habitats in the group. Vocal divergence closely followed the divergence of visual display. The vocalizations of most ornamented *crisatella* and *pygmaea* were most similar to each other compared with those of distantly related species. The vocalizations of basal species were most similar to that of a much-derived species of *Aethia*. Therefore, together with phylogenetic relatedness, a combination

of ecological and social factors appears to have produced the vocal affinities in these non-oscines.

ACKNOWLEDGEMENTS

We are grateful for the generous research support, assistance in the analysis, and feedback provided by Ted Miller for this study. We thank Jeff Williams and Vernon Byrd for logistic support and permission to conduct research in the Aleutian Island Unit of the Alaska Maritime National Wildlife Refuge; Grant Humphries, Chris Small, and Pamela Woodman for their assistance in the field; Dawn Marshall for the comments on the analysis; and Michael Rosenzweig and an anonymous reviewer for comments on the manuscript. The Macaulay Library of the Cornell Lab of Ornithology provided the recording equipment and technical assistance. We acknowledge the support provided by the captain and crew of the vessel *M/V Tiglax* for transportation in the Aleutian Islands. Natural Sciences and Engineering Research Council (NSERC) Canada – Discovery Grant held by I.L.J. provided the major funding. Support for the phylogenetic analyses was provided by a grants and contracts agreement from the Canadian Department of Fisheries and Oceans (DFO) to S.M.C.

REFERENCES

- Alström, P., Olsson, U., Rasmussen, P.C., Yao, C.T., Ericson, P.G.P. and Sundberg, P. 2007. Morphological, vocal and genetic divergence in the *Cettia acanthizoides* complex (Aves: Cettiidae). *Zool. J. Linn. Soc.*, **149**: 437–452.
- Athreya, R. 2006. A new species of *Liocichla* (Aves: Timaliidae) from Eaglenest Wildlife Sanctuary, Arunachal Pradesh, India. *Indian Birds*, **2**: 82–94.
- Atz, J.W. 1970. The application of the idea of homology to behavior. In *Development and Evolution of Behavior* (L.R. Aronson, E. Tobach, D.S. Lehrman and J.S. Rosenblatt, eds.), pp. 53–74. San Francisco, CA: Freeman.
- Badyaev, A.V. and Leaf, E.S. 1997. Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. *Auk*, **114**: 40–46.
- Baptista, L.F. and Schuchmann, K.L. 1990. Song learning in the Anna Hummingbird (*Calypte anna*). *Ethology*, **84**: 15–26.
- Baptista, L.F. and Trail, P.W. 1992. The role of song in the evolution of passerine diversity. *Syst. Biol.*, **41**: 242–247.
- Bertelli, S. and Tubaro, P.L. 2002. Body mass and habitat correlates of song structure in a primitive group of birds. *Biol. J. Linn. Soc.*, **77**: 423–430.
- Blumenrath, S.H. and Dabelsteen, T. 2004. Degradation of great tit (*Parus major*) song before and after foliation: implications for vocal communication in a deciduous forest. *Behaviour*, **141**: 935–958.
- Bradbury, J.W. and Vehrencamp, S.L. 1998. *Principles of Animal Communication*. Sunderland, MA: Sinauer Associates.
- Bradstreet, M.S.W. and Herter, D.R. 1990. *Seabird Colony Studies*. Anchorage, AK: US Fish and Wildlife Service, Alaska Regional Office.
- Burns, K. 1998. Molecular phylogenetics of the genus *Piranga*: implications for biogeography and the evolution of morphology and behavior. *Auk*, **115**: 621–634.
- Byrd, G.V. and Day, R.H. 1986. The avifauna of Buldir Island, Aleutian Islands. *Arctic*, **39**: 109–118.
- Cannell, P.F. 1988. Techniques for study of avian syrinxes. *Auk*, **100**: 289–293.
- Catchpole, C.K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour*, **74**: 149–166.
- Catchpole, C.K. 1982. The evolution of bird sounds in relation to mating and spacing behavior. In *Acoustic Communication in Birds* (D.E. Kroodsma and E.H. Miller, eds.), pp. 297–319. New York: Academic Press.

- Cuervo, A.M., Cadena, C.D. and Krabbe, N. 2005. *Scytalopus stilesi*, a new species of tapaculo (Rhinocryptidae) from the Cordillera Central of Colombia. *Auk*, **122**: 445–463.
- Cunningham, C.W., Omland, K.E. and Oakley, T.H. 1998. Reconstructing ancestral character states: a critical reappraisal. *Trends Ecol. Evol.*, **13**: 361–366.
- Drost, C.A. and Lewis, D.B. 1995. Xantus's Murrelet (*Synthliboramphus hypoleucus*). In *The Birds of North America*, No. 164 (A. Poole and F. Gill, eds.). Philadelphia, PA/Washington, DC: Academy of Natural Sciences/American Ornithologists' Union.
- Edwards, S.V., Kingan, S.B., Calkins, J.D., Balakrishnan, C.N., Jennings, W.B., Swanson, W.J. *et al.* 2005. Speciation in birds: genes, geography, and sexual selection. *Proc. Natl. Acad. Sci. USA*, **102**: 6550–6557.
- Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.*, **139**: S125–S153.
- Endler, J.A. 1993. Some general comments on the evolution and design of animal communication systems. *Phil. Trans. R. Soc. Lond. B*, **340**: 215–225.
- Farris, J.S. 1989. The retention index and the reseeded consistency index. *Cladistics*, **5**: 417–419.
- Friesen, V.L., Baker, A.J. and Piatt, J.F. 1996. Phylogenetic relationships within the Alcidae (Charadriiformes: Aves) inferred from total molecular evidence. *Mol. Biol. Evol.*, **13**: 359–367.
- Frumhoff, P.C. and Reeve, H.K. 1994. Using phylogenies to test hypotheses of adaptation: a critique of some current proposals. *Evolution*, **48**: 172–180.
- Gaston, A.J. and Jones, I.L. 1998. *The Auks*. Oxford: Oxford University Press.
- Hagelin, J.C. and Jones, I.L. 2007. Bird odors and other chemical substances: a defense mechanism or overlooked mode of intraspecific communication? *Auk*, **124**: 741–761.
- Hailman, J.P. and Ficken, M.S. 1996. Comparative analysis of repertoires, with reference to chickadees. In *Ecology and Evolution of Acoustic Communication in Birds* (D.E. Kroodsma and E.H. Miller, eds.), pp. 136–159. Ithaca, NY: Cornell University Press.
- Humphries, E.M. and Winker, K. 2010. Working through polytomies: auklet revisited. *Mol. Phylogenet. Evol.*, **54**: 88–96.
- Hunter, F.M., Jones, I.L., Williams, J.C. and Byrd, G.V. 2002. Breeding biology of the Whiskered Auklet (*Aethia pygmaea*) at Buldir Island, Alaska. *Auk*, **119**: 1036–1051.
- Irwin, R.E. 1996. The phylogenetic content of avian courtship display and song evolution. In *Phylogenies and the Comparative Method in Animal Behavior* (E.P. Martins, ed.), pp. 234–252. Oxford: Oxford University Press.
- Irwin, D.E. 2000. Song variation in an avian ring species. *Evolution*, **54**: 998–1010.
- Isler, M.L., Isler, P.R. and Whitney, B.M. 2007. Species limits in antbirds (Thamnophilidae): the Warbling Antbird (*Hypocnemis cantator*) complex. *Auk*, **124**: 11–28.
- Jarvis, E.D. 2006. Evolution of brain structures for vocal learning in birds: a synopsis. *Acta Zool. Sinica*, **52**: 85–89.
- Jones, I.L. 1993a. Crested Auklet (*Aethia cristatella*). In *The Birds of North America*, No. 70 (A. Poole and F. Gill, eds.). Philadelphia, PA/Washington, DC: Academy of Natural Sciences/American Ornithologists' Union.
- Jones, I.L. 1993b. Least Auklet (*Aethia pusilla*). In *The Birds of North America*, No. 69 (A. Poole and F. Gill, eds.). Philadelphia, PA/Washington, DC: Academy of Natural Sciences/American Ornithologists' Union.
- Jones, I.L. 1999. Assessing the role of sexual selection in adaptive radiation of the auklets (Alcidae, Aethiini). *Proc. Int. Ornithol. Congr.*, **22**: 1115–1125.
- Jones, I.L. and Hunter, A.J. 1993. Mutual sexual selection in a monogamous seabird. *Nature*, **362**: 238–239.
- Jones, I.L., Falls, J.B. and Gaston, A.J. 1987. Vocal recognition between parents and young of Ancient Murrelets (*Synthliboramphus antiquus*). *Anim. Behav.*, **35**: 1405–1415.
- Jones, I.L., Falls, J.B. and Gaston, A.J. 1989a. The vocal repertoire of the Ancient Murrelet. *Condor*, **91**: 699–710.

- Jones, I.L., Gaston, A.J. and Falls, J.B. 1989b. Factors affecting colony attendance by Ancient Murrelets (*Synthliboramphus antiquus*). *Can. J. Zool.*, **68**: 433–441.
- Jones, I.L., Konyukhov, N.B., Williams, J.C. and Byrd, G.V. 2001. Parakeet Auklet (*Aethia psittacula*). In *The Birds of North America*, No. 594 (A. Poole and F. Gill, eds.). Philadelphia, PA: The Birds of North America, Inc.
- Kaneshiro, K.Y. 1988. Speciation in the Hawaiian *Drosophila*: sexual selection appears to play an important role. *BioScience*, **38**: 258–263.
- King, A.S. 1989. Functional anatomy of the avian syrinx. In *Form and Function in Birds* (A.S. King and J. McLelland, eds.), pp. 105–192. London: Academic Press.
- Kluge, A.G. and Farris, J.S. 1969. Quantitative phylogenetics and the evolution of anurans. *Syst. Zool.*, **18**: 1–32.
- Kort, S.R.D. and ten Cate, C. 2004. Repeated decrease in vocal repertoire size in *Streptopelia* doves. *Anim. Behav.*, **67**: 549–557.
- Kroodsma, D.E. and Candy, R.A. 1985. Differences in repertoire size, singing behavior, and associated neuroanatomy among marsh wren populations have a genetic basis. *Auk*, **102**: 439–446.
- Lanyon, W.E. 1969. Vocal characters and avian systematics. In *Bird Vocalizations* (R.A. Hinde, ed.), pp. 291–310. Cambridge: Cambridge University Press.
- Maddison, W.P. and Maddison, D.R. 1992. *MacClade 3.04: Analysis of Phylogeny and Character Evolution*. Sunderland, MA: Sinauer Associates.
- Manuwal, D.A. and Thoresen, A.C. 1993. Cassin's Auklet (*Ptychorhamphus aleuticus*). In *The Birds of North America*, No. 50 (A. Poole and F. Gill, eds.). Philadelphia, PA/Washington, DC: Academy of Natural Sciences/American Ornithologists' Union.
- Marler, P. 1955. Characteristics of some animal calls. *Nature*, **176**: 6–7.
- Marler, P. and Pickert, R. 1984. Species-universal microstructure in the learned song of the swamp sparrow (*Melospiza georgiana*). *Anim. Behav.*, **32**: 673–689.
- Marler, P. and Slabbekoorn, H. 2004. *Nature's Music: The Science of Birdsong*. New York: Academic Press.
- Marten, K. and Marler, P. 1977. Sound transmission and its significance for animal vocalization. *Behav. Ecol. Sociobiol.*, **2**: 271–290.
- Marten, K., Quine, D. and Marler, P. 1977. Sound transmission and its significance for animal vocalization. *Behav. Ecol. Sociobiol.*, **2**: 291–302.
- Martens, J. 1996. Vocalizations and speciation of palearctic birds. In *Ecology and Evolution of Acoustic Communication in Birds* (D.E. Kroodsma and E.H. Miller, eds.), pp. 221–240. Ithaca, NY: Cornell University Press.
- Masters, J.C. 2007. Taking phylogenetics beyond pattern analysis: can models of genome dynamics guide predictions about homoplasy in morphological and behavioral data sets? *J. Human Evol.*, **52**: 522–535.
- McCracken, K.G. and Sheldon, F.H. 1997. Avian vocalizations and phylogenetic signal. *Proc. Natl. Acad. Sci. USA*, **94**: 3833–3836.
- Miller, E.H. 1996. Acoustic differentiation and speciation in shorebirds. In *Ecology and Evolution of Acoustic Communication in Birds* (D.E. Kroodsma and E.H. Miller, eds.), pp. 241–257. Ithaca, NY: Cornell University Press.
- Miller, E.H. and Baker, A.J. 2009. Antiquity of shorebird acoustic displays. *Auk*, **122**: 6–11.
- Miller, E.H., Seneviratne, S.S., Jones, I.L., Robertson, G.J. and Wilhelm, S.I. 2008. Syringeal anatomy and allometry in murrets (Alcidae: Uria). *J. Ornithol.*, **149**: 545–554.
- Morton, E.S. 1975. Ecological sources of selection on avian sounds. *Am. Nat.*, **109**: 17–34.
- Moum, T., Johansen, S., Erikstad, K.E. and Piatt, J.F. 1994. Phylogeny and evolution of the auks (subfamily Alcinae) based on mitochondrial DNA sequences. *Proc. Natl. Acad. Sci. USA*, **91**: 7912–7916.
- Nelson, S.K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). In *The Birds of North America*,

- No. 276 (A. Poole and F. Gill, eds.). Philadelphia, PA/Washington, DC: Academy of Natural Sciences/American Ornithologists' Union.
- Nicholls, J.A. and Goldizen, A.W. 2006. Habitat type and density influence vocal signal design in satin bowerbirds. *J. Anim. Ecol.*, **75**: 549–558.
- Nottebohm, F. 1972. The origins of vocal learning. *Am. Nat.*, **106**: 116–140.
- Omland, K.E. and Lanyon, S.M. 2000. Reconstructing plumage evolution in orioles (*Icterus*): repeated convergence and reversal in patterns. *Evolution*, **54**: 2119–2133.
- Päckert, M., Martens, J., Kosuch, J., Nazarenko, A.A. and Veith, M. 2003. Phylogenetic signal in the song of crests and kinglets (Aves: Regulus). *Evolution*, **57**: 616–629.
- Park, O., Barden, A. and Williams, E. 1940. Studies in nocturnal ecology IX: Further analysis of activity of Panama rain forest animals. *Ecology*, **21**: 122–134.
- Paton, T.A. and Baker, A.J. 2006. Sequences from 14 mitochondrial genes provide a well-supported phylogeny of the charadriiform birds congruent with the nuclear RAG-1 tree. *Mol. Phylogenet. Evol.*, **39**: 657–667.
- Paton, T., Baker, A.J., Groth, J.G. and Barrowclough, G.F. 2003. RAG-1 sequences resolve phylogenetic relationships within charadriiform birds. *Mol. Phylogenet. Evol.*, **29**: 268–278.
- Payne, R.B. 1986. Bird songs and avian systematics. *Curr. Ornithol.*, **3**: 87–126.
- Pereira, S.L. and Baker, A.J. 2008. DNA evidence for a Paleocene origin of the Alcidae (Aves: Charadriiformes) in the Pacific and multiple dispersals across northern oceans. *Mol. Phylogenet. Evol.*, **46**: 430–445.
- Podos, J. and Nowicki, S. 2004. Beaks, adaptation, and vocal evolution in Darwin's finches. *Bioscience*, **54**: 501–510.
- Price, J.J. and Lanyon, S.M. 2002. Reconstructing the evolution of complex bird song in the oropendolas. *Evolution*, **56**: 1514–1529.
- Price, T. 1997. Correlated evolution and independent contrasts. *Phil. Trans. R. Soc. Lond. B*, **352**: 519–529.
- Seddon, N. 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution*, **59**: 200–215.
- Seneviratne, S.S. 2009. On the evolutionary and ecological significance of ornamental traits: the function and variability of some of the acoustic and visual displays in Aethiini. PhD dissertation, Memorial University, St. John's, Canada.
- Seneviratne, S.S. and Jones, I.L. 2008. Mechanosensory function for facial ornamentation in the whiskered auklet, a crevice-dwelling seabird. *Behav. Ecol.*, **19**: 784–790.
- Seneviratne, S.S. and Jones, I.L. 2010. Origin and maintenance of mechanosensory feather ornaments. *Anim. Behav.*, **79**: 637–644.
- Seneviratne, S.S., Jones, I.L. and Miller, E.H. 2009. Vocal repertoires of auklets (Alcidae: Aethiini): structural organization and categorization. *Wilson J. Ornithol.*, **121**: 568–584.
- Slabbekoorn, H., Kort, S.D. and ten Cate, C. 1999. Comparative analysis of perch-coo vocalizations in *Streptopelia* doves. *Auk*, **116**: 737–748.
- Strauch, J.G. 1985. The phylogeny of the Alcidae. *Auk*, **102**: 520–539.
- Swofford, D.L. 2002. *PAUP: Phylogenetic Analysis Using Parsimony*, Version 4.0b. Sunderland, MA: Sinauer Associates.
- Thomas, G.H., Wills, M.A. and Székely, T. 2004. A supertree approach to shorebird phylogeny. *BMC Evol. Biol.*, **4**: 28.
- Thoresen, A. 1964. The breeding behavior of the Cassin's Auklet. *Condor*, **66**: 456–476.
- Tobias, J.A., Aben, J., Brumfield, R.T., Derryberry, E.P., Halfwerk, W., Slabbekoorn, H. *et al.* 2010. Song divergence by sensory drive in Amazonian birds. *Evolution*, **64**: 2820–2839.
- Uy, J.A.C. and Borgia, G. 2000. Sexual selection drives rapid divergence in bowerbird display traits. *Evolution*, **54**: 273–278.
- Walsh, H.E., Kidd, M.G., Moum, T. and Friesen, V.L. 1999. Polytomies and the power of phylogenetic inference. *Evolution*, **53**: 932–937.

- Warner, R.W. 1969. The anatomy of the avian syrinx. PhD dissertation, University of London, London.
- Westoby, M., Leishman, M.R. and Lord, J.M. 1995. On misinterpreting the 'phylogenetic correction'. *J. Ecol.*, **83**: 531–534.
- Wiley, R.H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. *Am. Nat.*, **138**: 973–993.
- Wiley, R.H. and Richards, D.G. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In *Acoustic Communication in Birds: Production, Perception, and Design Features of Sounds* (D.E. Kroodsma and E.H. Miller, eds.), pp. 131–181. New York: Academic Press.
- Wimberger, P.H. and Queiroz, A.D. 1996. Comparing behavioral and morphological characters as indicators of phylogeny. In *Phylogenies and the Comparative Method in Animal Behavior* (E.P. Martins, ed.), pp. 206–233. Oxford: Oxford University Press.
- Zubakin, V.A. and Konyukhov, N.B. 1999. Biology of reproduction of the Whiskered Auklet (*Aethia pygmaea*): pattern of nesting, activity in the colony, and social behavior. *Biol. Bull.*, **26**: 460–468.

APPENDIX

Summary of vocal characters (both acoustic and syringeal characters) and character states used in the phylogenetic comparison

Acoustic characters

1. Number of note types in the repertoire: 0 = ≤ 5 , 1 = > 5
2. Minimum note length: 0 = < 20 ms, 1 = 20–30 ms, 2 = > 30 ms
3. Maximum note length: 0 = < 500 ms, 1 = 500–1500 ms, 2 = > 1500 ms
4. Minimum F_{μ} : 0 = < 1.0 kHz, 1 = 1.0–1.5 kHz, 2 = > 1.5 kHz
5. Maximum F_{μ} : 0 = < 2.5 kHz, 1 = 2.5–4.0 kHz, 2 = > 4.0 kHz
6. Most expressed harmonic: 0 = F_0 , 1 = F_1 , F_2 or F_3 , 2 = variable
7. Minimum F_0 : 0 = > 1.5 kHz, 1 = < 1.5 kHz
8. Greatest number of frequency peaks in a note: 0 = < 20 , 1 = 20–40, 2 = > 40
9. Minimum frequency modulation (FM) in a note: 0 = < 0.6 kHz, 1 = > 0.6 kHz
10. Maximum FM in a note: 0 = < 1.5 kHz, 1 = 1.50–2.25 kHz, 2 = > 2.25 kHz
11. Number of vocalization types in repertoire: 0 = ≤ 4 , 1 = > 4
12. Maximum length of vocalization: 0 = > 22 s, 1 = < 22 s
13. Minimum length of vocalization: 0 = > 2.2 s, 1 = < 2.5 s
14. Maximum number of note types in a vocalization: 0 = < 5 , 1 = > 5
15. Minimum note spacing in a vocalization: 0 = > 10 ms, 1 = < 10 ms
16. Level of structural organization in vocalization: 0 = lengthy, continuous, poorly defined, 1 = brief and differentiated into introduction, body, end
17. Presence of pulses (brief note types) in vocalization: 0 = present, 1 = absent
18. Presence of pure tones: 0 = absent, 1 = present
19. Presence of trills (note types with very rapid FM): 0 = absent, 1 = present
20. Presence of broadband noise: 0 = present, 1 = absent
21. Presence of FM along carrier frequency in the display: 0 = high, 1 = low
22. Alternate and repeated arrangement of several note types in vocalization: 0 = present, 1 = absent

23. Sequentially graded note type arrangement in vocalization: 0 = present, 1 = predominant
24. Clustered arrangement of notes in vocalization: 0 = present, 1 = absent
25. Formation of rafts and associated vocalization at sea: 0 = absent, 1 = present
26. Aerial vocalization: 0 = present, 1 = absent
27. Synchronous vocalization by several birds at the colony: 0 = predominant, 1 = rare
28. Duet (display delivered by two individuals where each participant contributes to a specific section): 0 = present, 1 = absent

Syringeal characters

29. Syringeal width: 0 = <4.4 mm, 1 = ≥4.4 mm
30. Mean syringeal depth: 0 = <4.8 mm, 1 = ≥4.8 mm
31. Mean width of m. tracheolateralis: 0 = <0.9 mm, 1 = ≥0.9 mm
32. Mean width of m. sternotrachealis: 0 = <1.6 mm, 1 = ≥1.6 mm
33. Number of calcified tracheal rings: 0 = >5 rings, 1 = ≤5 rings
34. Completely calcified tracheal rings: 0 = present, 1 = absent
35. Ventral syringeal calcification: 0 = present, 1 = absent
36. Dorsal syringeal calcification: 0 = >5 rings, 1 = ≤5 rings
37. Fused calcified rings: 0 = present, 1 = absent
38. Calcification of pessulus: 0 = complete, 1 = partial