

## VOCAL REPERTOIRES OF AUKLETS (ALCIDAE: AETHIINI): STRUCTURAL ORGANIZATION AND CATEGORIZATION

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**ABSTRACT.**—We categorized and quantified the complete vocal repertoires of breeding adult auklets (Aethiini, 5 species) in their breeding areas to provide a baseline for comparative study of the structure and function of vocalizations within this monophyletic group of seabirds. We recognized 22 call types across species and 3–5 call types for each species. Calls were characterized by one to five frequency modulated, harmonically rich note types arranged sequentially in varied combinations. Frequency attributes varied more than temporal attributes within and across species. Repertoires and display complexity of nocturnal and diurnal species did not differ consistently. We recognized two major forms of vocal display: alternating arrangement of note types (Cassin's Auklet [*Ptychoramphus aleuticus*] and Parakeet Auklet [*Aethia psittacula*]); and sequentially graded arrangement of note types (Least Auklet [*A. pusilla*] and Whiskered Auklet [*A. pygmaea*]). One species' repertoire (Crested Auklet [*A. cristatella*]) was composed of a mix of the two forms of display. There were vocal homologies in frequency modulation of notes, arrangement of notes, and note type composition of displays. Our analysis revealed vocal similarities between: (1) two species not normally grouped together (Cassin's and Parakeet auklets); and (2) Whiskered and Crested auklets, which have been suggested previously to be closely related. Received 18 January 2008. Accepted 3 February 2009.

Vocal and other animal displays typically are correlates of speciation and population divergence (Lanyon 1969; Payne 1986; Martens 1996; Price and Lanyon 2002; Isler et al. 2005, 2007), and are used routinely in modern species-level systematics (Cuervo et al. 2005, Athreya 2006, Gonzaga et al. 2007). Vocalizations that are not learned are likely to be especially informative in elucidating relationships; those vocalizations are widespread as they typify most non-passerine bird families (Baptista and Schuchmann 1990, Farabaugh and Dooling 1996, Price and Lanyon 2002, Jarvis 2006). Some vocal traits likely represent convergence due to selection for effective transmission in similar habitats (McCracken and Sheldon 1997, Seddon 2005), and some vocal homoplasies could occur due to similar functions in different acoustic environments (Marler 1955). Most studies of vocal relationships between species have used single vocal homologues (Davis 1962, 1965; Winkler and Short 1978; Slabbekoorn et al. 1999; Seddon 2005; Shelley and Blumstein 2005), but a few have used entire repertoires (Price and Lanyon 2002). The latter approach is preferable because analysis of at least a few sound classes is necessary to understand acoustic differentiation in groups with complex vocalizations or large repertoires (Price and Lanyon 2002, Isler et al. 2007).

The Alcidae (subfamily Alcinae; Thomas et al. 2004) diverged from the lineage leading to skuas and jaegers (*Skua* and *Stercorarius*; Paton et al. 2003, Thomas et al. 2004, Paton and Baker 2006, Fain and Houde 2007) about 60 Mya (Pereira and Baker 2008). Relationships among the auklets (tribe Aethiini) remain unclear, but it is agreed the five extant species constitute a monophyletic group: Cassin's Auklet (*Ptychoramphus aleuticus*), Crested Auklet (*Aethia cristatella*), Least Auklet (*A. pusilla*), Parakeet Auklet (*A. psittacula*), and Whiskered Auklet (*A. pygmaea*) (Strauch 1985, Mouton et al. 1994, Friesen et al. 1996, Thomas et al. 2004).

Auklets are highly vocal at their breeding colonies, and mixed-species colonies are nearly universal in Alaska. The social environments of auklets are similar across species: they are colonial and socially monogamous, and males and females are nearly identical in plumage and body size. Only Cassin's and (in most colonies) Whiskered auklets are nocturnally active. However, they inhabit acoustically diverse habitats (Jones 1993a, b; Manuwal and Thoresen 1993; Gaston and Jones 1998; Jones 1999; Jones et al. 2001), and divergent adaptations to different physical environments are possible (Endler 1993, Nicholls et al. 2006). For example, four auklet species breed in rocky habitats or on cliffs, but Cassin's Auklets breed on slopes with soft earth, covered with dense grass and occasionally trees (Thoresen 1964, Manuwal and Thoresen 1993).

We conducted a comparative study of auklet vocalizations to elucidate vocal relationships

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among auklet species; this is the first comparative study for the Alcidae. The objectives of our study were to: (1) quantify and characterize the structural organization of vocal repertoires, (2) relate vocal repertoires to species differences in phylogeny and ecology, and (3) identify vocal displays of significance to conservation-restoration projects. We describe vocalizations and vocal behavior, standardize terminology, and identify possible applications.

## METHODS

*Study Sites and Recording Methods.*—Recordings were made in the Aleutian Islands, Alaska: Buldir Island (52° 22' N, 175° 54' E), 25 May to 7 June 2005 and 25 May to 24 July 2006; and Egg Island (53° 52' N, 166° 03' W), 15 June to 11 July 2005. Both are grass-covered, treeless volcanic islands with beach boulders and exposed talus slopes, and large breeding colonies of auklets (Byrd and Day 1986, Bradstreet and Herter 1991). All five auklet species breed on Buldir Island; Cassin's, Parakeet, and Whiskered Auklets breed on Egg Island.

Recordings were made opportunistically during times of peak activity: Cassin's Auklet, 0200–0500 hrs (Aleutian standard time); Crested and Least auklets, 0900–1400 hrs; Parakeet Auklet, 0600–1200 hrs; and Whiskered Auklet, 1800–0200 and 0400–0600 hrs. We recorded birds separated by at least 10 m to minimize the possibility of recording individuals more than once. Cassin's and Whiskered auklets were recorded at night with the aid of a red lithium electrode diode headlamp (Zubakin and Konyukhov 1999). All recordings were of undisturbed birds.

*Equipment.*—We recorded birds with a Sony TCD-D10PROII Digital Audio Tape recorder (sampling rates 32, 44.1, or 44.2 kHz), or Fostex FR-2 solid-state recorder (sampling rate 48.1 kHz) with Sennheiser MKH 70 or MKH 816 directional microphones (with wind guard and wind sock) and 3–30 m cables. Microphones were tripod-mounted or hand-held. Recording sessions with individual birds were 30 min to 3 hrs in duration and contained multiple continuous recordings of 2–10 min in duration, each accompanied by behavioral observations. We recorded birds at distances of ~2–6 m and recording sessions totaled ~80 hrs.

All birds were assumed to be breeding adults as calling birds are mostly adults, and adults

predominate at colony sites in the early and mid breeding season (Jones 1993a, b; Manuwal and Thoresen 1993; Jones et al. 2001; Zubakin and Konyukhov 2001). Gender of calling birds was known only for Crested Auklets, based on the distinctive bill shape and courtship display (Jones 1993c).

*Acoustic Description and Measurement.*—We selected recordings of good quality for analysis with Raven 1.2.1 (Bioacoustics Program, Cornell Laboratory of Ornithology, Ithaca, NY, USA). Blackman window was used for all analyses. Other analytical settings for Cassin's and Parakeet auklets were: window size, 800 samples; 3 dB filter bandwidth, 90.5 Hz; time grid overlaps, 75%; and frequency grid spacing, 43.1 Hz. Corresponding settings for Crested and Whiskered auklets were 512 samples, 141 Hz, 90%, and 86.1 Hz; and for Least Auklet were 250 samples, 289 Hz, 50%, and 172 Hz. The dominant harmonic was judged from the spectrogram slice view.

We used a combination of audible differences, overall visual impressions of vocal sequences, and constituent sound notes on spectrograms (Marler and Pickert 1984, Jones et al. 1989, Hailman and Ficken 1996, Marler and Slabbekoorn 2004, Seddon 2005), and explicit measurements of physical properties to characterize vocal repertoires. We referred to classes of basic sound elements as "notes" following Marler and Pickert (1984), and Marler and Slabbekoorn (2004). We recognized note types to separate overall acoustic variation, and to characterize overall acoustic diversity within species, rather than to approximate natural display classes. We pooled brief elements (e.g., the first 3 in Fig. 1A [a, b, a]) as a single note type (note type V), separated graded series into several note types (e.g., note types I and III in Fig. 1A), and pooled acoustically similar parts of different calls (e.g., note types II and III in Fig. 1A, C).

We measured duration, frequency, modulation of the carrier frequency, and harmonic structure ( $F_n$ , frequency of  $n^{\text{th}}$  harmonic;  $F_0$ , fundamental frequency;  $F_{\mu}$ , frequency of the most strongly expressed harmonic [i.e., the harmonic with the highest intensity in the power spectrum];  $CF_n$ , carrier frequency of the  $n^{\text{th}}$  harmonic; and FM, frequency modulation of CF). Frequency was estimated from spectrograms by selecting the beginning, end, highest, and lowest points of the signal. The frequency of the signal is that of the

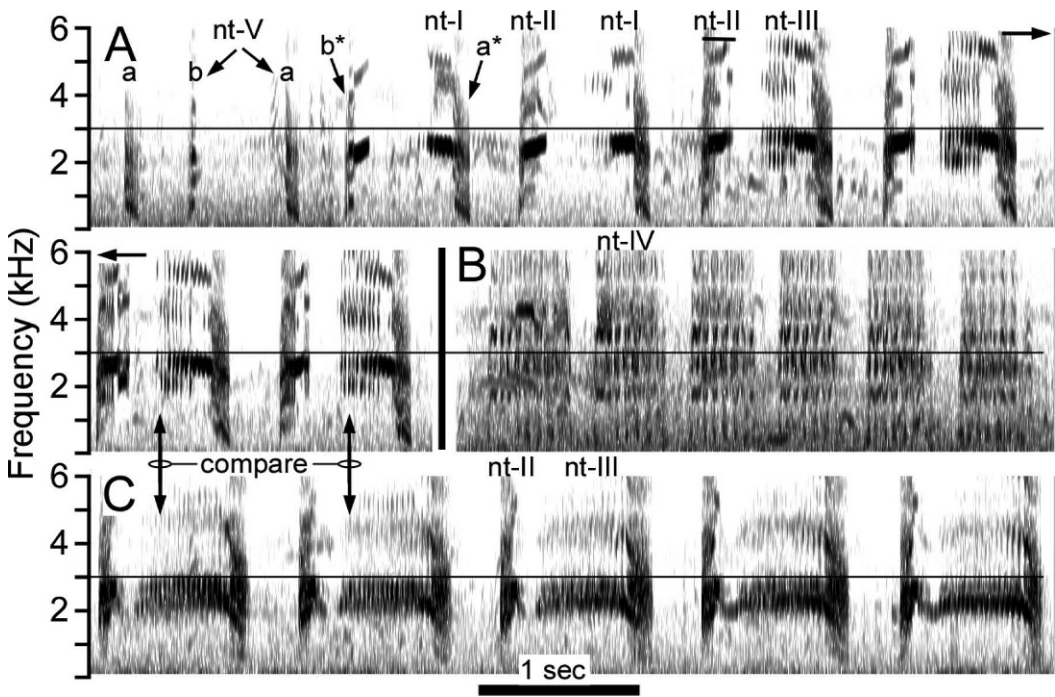


FIG. 1. Calls of Cassin's Auklet. (A) *Kut-I-eer* (two panels). The last three (a, b, a) of a long series of introductory notes are shown. Some note types (nt-) are marked on this and other panels. Introductory notes correspond to the beginning (b\*) and end (a\*) of each note couplet in the high-intensity portion of the call. (B) *Kreerr-er*. The first faint note is not shown. (C) *Kut-reeah* (section of the high-intensity portion of an 18-sec long call). The 3-kHz line is a visual guide.

selected rectangle's center (in Raven). We estimated FM by selecting the lowest and highest frequencies of the signal, and taking the frequency difference between these two points from the selection table (in Raven). Display types were identified for each species based on the composition of note types and audible plus visual characteristics, most of which were easily and reliably distinguishable in the field. Our nomenclature partly follows previous published descriptions (Thoresen 1964; Byrd and Williams 1993; Jones 1993a, b; Manuwal and Thoresen 1993; Jones et al. 2001), but we provide new names for previously unrecognized call types.

## RESULTS

Auklet repertoires encompassed 22 call types, which were built on 1–5 frequency modulated and harmonically rich note types (28 types across species) arranged sequentially in varied combinations (Fig. 1). Most notes were strongly harmonic, brief, and with pronounced FM (Table 1, Fig. 1). Characteristics of notes and their organization in displays were uniform within species.

*Cassin's Auklet*.—Adults had three kinds of calls, all with harsh screeching qualities; some were long (~50 sec). They ranged from 2 to 50 sec (means = 4–18 sec). All calls consisted of rhythmically repeated notes or note couplets; the latter appear to represent vocalizations during alternating inspirations and expirations. The low number of call types was paralleled by little structural diversity across the five note types we recognized (e.g.,  $F_{\mu}$  varied only from 2.2 to 3.1 kHz; Table 1). Call types differed little in diversity (range = 2–4 note types).

*Kut-I-eer* (I) (Fig. 1A; Tables 1, 2). This long complex call began and ended with simple notes, which graded into a more complex main part. The introductory note series at times was long (~300 msec); the terminal series was brief. This call was structured on note couplets, which were apparent even in the introductory and terminal note series. The brief introductory notes marked as “a” and “b” (Fig. 1A, representing note type V) are structurally identical to the termination (e.g., a\*) and beginning (e.g., b\*), respectively, of the more complex notes in the main portion of the

TABLE 1. Descriptive statistics ( $\bar{x} \pm SD$ , range) for call duration, frequency measures, and harmonic structure for note types of auklets (Aethini).  $F_{\mu}$ , most strongly expressed frequency; FM, frequency modulation of  $F_{\mu}$ ;  $F_0$ , fundamental frequency; and  $F_n$ , frequency of  $n^{\text{th}}$  harmonic.

Species	Note type (nt)	Duration (msec)	$F_{\mu}$ (kHz)	FM (kHz)	$F_{\mu}$	Harmonic structure	$n$
Cassin's	I	225 $\pm$ 52 (135–305)	2.2 $\pm$ 0.17 (1.9–2.4)	1.0 $\pm$ 0.39 (0.6–2.0)	$F_0$	Weak	10
	II	560 $\pm$ 263 (285–1,075)	2.3 $\pm$ 0.25 (1.9–2.7)	1.1 $\pm$ 0.58 (0.5–2.0)	$F_0$	Strong	10
	III	655 $\pm$ 145 (495–1,015)	2.5 $\pm$ 0.21 (2.1–2.8)	1.1 $\pm$ 0.31 (0.6–1.4)	$F_0$	Strong	11
	IV	170 $\pm$ 25 (135–230)	2.3 $\pm$ 0.19 (2.0–2.6)	1.4 $\pm$ 0.42 (0.8–2.1)	$F_0$	Strong	11
	V	35 $\pm$ 8 (20–45)	3.1 $\pm$ 0.39 (1.6–3.5)	0.5 $\pm$ 0.09 (0.4–0.6)	$F_0$ – $F_3$	Strong	7
Parakeet	I	45 $\pm$ 25 (20–115)	2.1 $\pm$ 0.56 (1.6–3.3)	1.2 $\pm$ 0.36 (0.7–2.0)	$F_0$	Weak	12
	II	60 $\pm$ 28 (25–120)	5.7 $\pm$ 0.18 (0.4–1.0)	0.4 $\pm$ 0.10 (0.3–0.6)	$F_0$	Strong	10
	III	1,250 $\pm$ 465 (750–1,950)	2.9 $\pm$ 0.30 (2.3–3.5)	2.2 $\pm$ 0.41 (1.8–2.9)	$F_0$	Strong	10
	IV	375 $\pm$ 103 (255–610)	0.5 $\pm$ 0.04 (0.5–0.6)	0.5 $\pm$ 0.06 (0.4–0.6)	$F_0$	Strong	10
Crested	I	170 $\pm$ 40 (110–255)	1.4 $\pm$ 0.49 (0.6–2.1)	0.7 $\pm$ 0.18 (0.3–0.9)	$F_0$ – $F_2$	Weak	10
	II	90 $\pm$ 50 (45–220)	1.6 $\pm$ 0.29 (1.1–2.1)	0.6 $\pm$ 0.18 (0.4–0.9)	$F_0$ – $F_2$	Weak	11
	III	730 $\pm$ 190 (510–1,030)	1.1 $\pm$ 0.12 (0.9–1.3)	0.6 $\pm$ 0.01 (0.4–0.7)	$F_0$ – $F_2$	Weak	10
	IV	340 $\pm$ 120 (180–755)	1.5 $\pm$ 0.23 (1.2–2.3)	1.1 $\pm$ 0.17 (0.2–1.2)	$F_0$ – $F_2$	Strong	20
	V	360 $\pm$ 128 (170–505)	1.6 $\pm$ 0.59 (0.6–2.0)	0.5 $\pm$ 0.13 (0.2–0.7)	$F_0$ – $F_2$	Weak	10
Whiskered	I	45 $\pm$ 17 (25–80)	3.4 $\pm$ 0.25 (2.8–3.9)	0.9 $\pm$ 0.30 (0.4–1.5)	$F_3$	Strong	20
	II	230 $\pm$ 82 (140–380)	3.8 $\pm$ 0.27 (3.5–4.3)	1.1 $\pm$ 0.26 (0.8–1.5)	$F_3$	Strong	10
	III	150 $\pm$ 35 (100–200)	4.0 $\pm$ 0.44 (3.2–4.7)	1.6 $\pm$ 0.34 (1.2–2.1)	$F_3$	Strong	10
	IV	315 $\pm$ 94 (190–510)	4.0 $\pm$ 0.30 (3.6–4.4)	1.5 $\pm$ 0.28 (1.1–2.0)	$F_3$	Strong	10
	V	190 $\pm$ 62 (40–280)	3.7 $\pm$ 0.43 (2.7–4.3)	1.1 $\pm$ 0.18 (0.7–1.3)	$F_3$	Strong	10
	VI	540 $\pm$ 99 (460–675)	3.5 $\pm$ 0.36 (2.9–3.8)	0.7 $\pm$ 0.23 (0.6–1.0)	$F_3$	Weak	5
	VII	545 $\pm$ 114 (370–690)	4.0 $\pm$ 0.27 (3.6–4.2)	1.7 $\pm$ 0.18 (1.4–1.9)	$F_3$	Strong	5
	VIII	435 $\pm$ 112 (270–515)	3.1 $\pm$ 0.13 (2.9–3.2)	0.7 $\pm$ 0.26 (0.3–1.0)	$F_3$	Strong	4
	IX	300 $\pm$ 29 (270–320)	3.8 $\pm$ 0.60 (3.5–4.5)	1.8 $\pm$ 0.29 (1.6–2.1)	$F_3$	Weak	3
	X	15 $\pm$ 4 (10–25)	3.5 $\pm$ 0.79 (3.1–5.7)	1.1 $\pm$ 0.30 (0.7–1.6)	$F_0$ – $F_1$	Strong	10
Least	I	40 $\pm$ 11 (25–55)	3.8 $\pm$ 0.11 (2.8–5.6)	1.1 $\pm$ 0.26 (0.6–1.5)	$F_0$ – $F_2$	Strong	9
	II	70 $\pm$ 18 (45–105)	4.0 $\pm$ 0.95 (3.0–5.3)	1.8 $\pm$ 1.39 (0.7–5.5)	$F_0$ – $F_3$	Strong	10
	III	125 $\pm$ 17 (90–150)	4.3 $\pm$ 0.89 (3.3–5.3)	2.3 $\pm$ 0.61 (1.4–3.0)	$F_0$ – $F_4$	Strong	10
	IV	370 $\pm$ 77 (265–515)	3.5 $\pm$ 0.33 (3.2–4.0)	1.4 $\pm$ 0.45 (1.0–2.5)	$F_0$	Weak	10



TABLE 3. Occurrence of auklet vocal displays in special, temporal, and behavioral situations. Qualitative score for the occurrence of the display in the given context: \*\*\* predominant; \*\* common; \*rare, (\*) occurrence is likely.

Auklet species	Display	Occurrence								
		Time		At the colony			Social interactions			
		Day	Night	Surface	In crevice	At sea	In flight	Courting	Advertisement	Contact/alarm
Cassin's	<i>Kut-I-er</i>		***	*	***			***	**	(**)
	<i>Kut-reearh</i>		***		***				***	
	<i>Kree-er</i>		***				***			***
Parakeet	<i>Whinny</i>	***	*	***	*			***	***	
	<i>Raft Whinny</i>	***	*			***		(**)	***	
	<i>Short Whinny</i>	***		**	***	**		(**)	(**)	
	<i>Chip</i>	***		**	***					**
	<i>Squeal</i>	**				**	***			***
Crested	<i>Cackle</i>	***	*	***	**	*		***		
	<i>Trumpet</i>	***	*	***	**	*		**	***	
	<i>Hoot</i>	***	*	*	***				***	
	<i>Whine</i>	**	**		***					***
	<i>Bark</i>	**		***	***	***	***			***
Whiskered	<i>Duet Beedoo</i>		***	*	***	**		***		(*)
	<i>Metallic Beedoo</i>		***	***	***	**		(**)	***	
	<i>Staccato Beedoo</i>		***	***	***	***		(*)	***	
	<i>Mew</i>	**	***	***	***	*				***
Least	<i>Bark</i>		*				**			**
	<i>Chatter</i>	**		***				**	***	
	<i>Deep chatter</i>	**		***				*	***	
	<i>Chirp</i>	***	*	**		***	***			***
	<i>Chirr-buzz</i>	**	*	***	**					***

call (broadband, brief, tonal with variable noise, and frequency decreasing or increasing). The first note of these complex couplets shifted from a brief introduction (b\*) to a frequency increasing tonal section. The second note began after a brief interval at about the same frequency as the first note ended, as a rapidly modulated (pulsed) frequency decreasing tone, which shifted to the terminal portion (e.g., a\*). The silent interval within couplets decreased as the call progressed. We interpret the *Kut* portion to occur on expiration, and *eer* to represent inspiration. *Kut-I-er* was the most common call and was delivered as single utterances, as duets, or in group displays (“*Kreek* chorus”) from within the breeding burrow at night (Table 3).

*Kreerr-er* (II) (Fig. 1B; Tables 1, 2). This fairly brief and simple (2 note types) call was a series of 6–10 notes. Each note consisted of 5–10 broadband pulses. It sounded like a rapid “*kreer...er...kreer...er...*”. This call at times was performed as a duet; single notes like those in this call type were used as flight calls at night, mostly by birds departing the colony (Table 3).

*Kut-reeah* (III) (Fig. 1C; Tables 1, 2). This call was intermediate in duration. Two alternating

note types were expressed (analogized as types II and III) at low to medium intensity, leading to repeated note couplets (first part, expiratory; second part, inspiratory). The notes joined (e.g., right notes in Fig. 1C) at high intensity. The first note (or first part of joined notes) was broadband and of high amplitude; the second note ended similarly, but began with a long pulsed portion, increasing the similarity to the *Kut-I-er* call (marked “compare”; Fig. 1). This relatively uncommon call was delivered as an advertisement display (i.e., a loud, medium- to long-distance display) uttered singly or in group displays from breeding burrows (Table 3).

*Parakeet Auklet*.—We recognized five call types in adults, which contained three to four structurally diverse types of pulsed, broadband, and tonal notes. Call duration was briefer than in Cassin's Auklet and ranged from 1 to 23 sec (means = 4–12 sec). The structure of some call types suggests phonation during successive expirations and inspirations within calls, as in Cassin's and Crested auklets.

*Chip* (I) (Fig. 2A; Tables 1, 2). This call type consisted of rhythmically alternating series of broadband pulses and single brief low-frequency

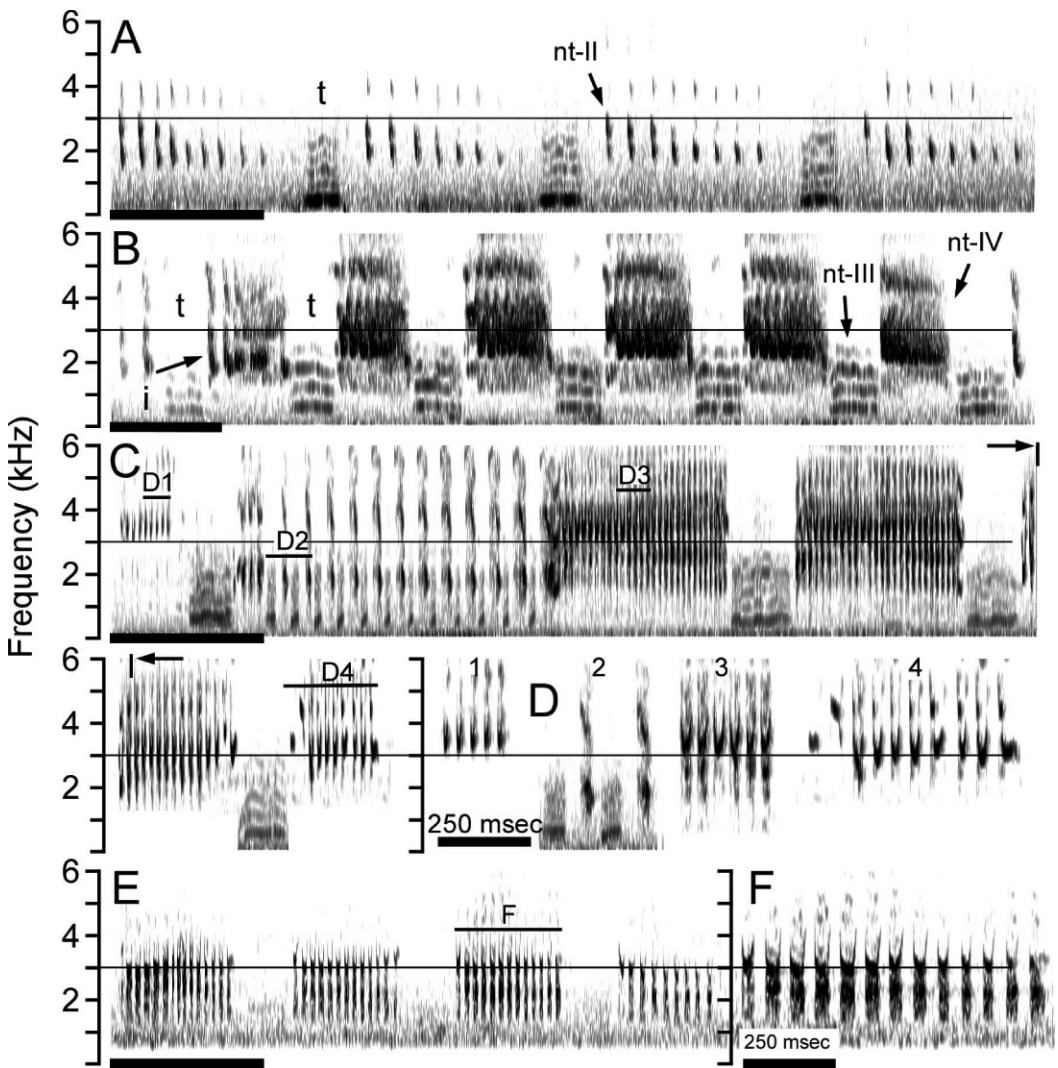


FIG. 2. Calls of Parakeet Auklet. (A) *Chip* (part of longer series); first tonal note is marked (t). Some note types (nt-) are marked. (B) *Whinny*; the first two tonal notes are marked (arrow emphasizes structural grading). (C) *Short Whinny* (over 2 panels). (D) Parts of panel C on different time scale. (E) *Raft Whinny* (part of longer series). (F) Part of panel (E) on different time scale. All time scales are 1.0 sec, except as marked. The 3-kHz line is a visual guide.

tonal notes. A similar arrangement was present in *Whinny* and *Short Whinny* calls, suggesting alternating exhalation (tonal note) and inhalation. The call sounded like “*kut..kut..kut..*”. It was delivered as a contact or as an alarm call (Table 3) from inside crevices and in front of entrances to burrows or crevices.

*Whinny* (II) (Fig. 2B; Tables 1, 2). This was the most common vocalization. It began and ended with brief broadband notes. The last of the introductory (*i*) notes (Fig. 2B) is followed by a

soft low-frequency tonal note (*t*) and a burst of loud higher-frequency pulses (compare structural similarity between note *i* and first pulse in Fig. 2B; the graded transition is marked by an arrow). Two note types alternate: a soft, low-frequency tonal note and a louder modulated (pulsed) note. This call sounded like a nasal “*hiph..phee..*”. It was performed mainly as a duet (Table 3).

*Short Whinny* (III) (Fig. 2C, D; Tables 1, 2). This call was comparatively brief (mean duration

= 4 sec), but complex (4 diverse note types). The example (Fig. 2C) began with a brief rapid trill (also "1" in Fig. 2D) followed by a tonal note as in the *Whinny* call (first *t*), another brief trill of three plus pulses, and a series of couplets of brief tonal and broadband sounds. The main part of the call was a series of alternating loud pulsed trills and tonal notes. Dominant frequency and rate of repetition within trills declined toward the end of the call. Notes within trills began with a sharp downsweep in frequency and ended with a sharp upsweep (Fig. 2D). This call was delivered singly or as a duet (Table 3).

*Raft Whinny* (IV) (Fig. 2E, F; Tables 1, 2). This call was about the same duration as the *Short Whinny*, but simpler. It consisted of a rhythmically repeated series of pulsed trills. The notes constituting the trills were brief and broadband; frequency attributes resembled those in the *Short Whinny* call. This call was uttered only in rafts of 10–25 birds swimming close together (Table 3).

*Squeal* (V) (not illustrated). This call had the audible quality of a squeal. It was given by disturbed birds taking flight, especially in the presence of predators (primarily Glaucous-winged Gull [*Larus glaucescens*] at Buldir Island, and Peregrine Falcon [*Falco peregrinus*] at Egg Island; Table 3). Birds also squealed when caught in mist nets.

*Crested Auklet*.—We recognized five call types for adults. They included a variety of barking, hooting, and cackling sounds, which were briefer than those of Cassin's and Parakeet auklets, but similar in duration to those of Whiskered Auklets (range = <1–10 sec; means = 0.4–8 sec). Most call variation was expressed in harmonic richness and duration, and calls lacked complex note-type arrangements as for Parakeet Auklets. Only this species produced fairly long tonal sounds. The structure of some call types suggests phonation during successive expirations and inspirations within calls as in Cassin's and Parakeet auklets.

*Trumpet* (I) (Fig. 3A, B; Tables 1, 2). This brief call was structurally well defined. It began with several long, tonal notes with strong  $F_0$  and few harmonics; these notes increased successively in duration and amplitude. The last of these notes (*kuhoo*) showed a distinctive terminal rise in frequency. It then shifted to a much lower  $F_0$  (from >2 kHz to ~650 Hz in the example (Fig. 3A), and then changed to a tonal section ( $F_0$  ~1.4 kHz; first *t* in Fig. 3B) that resembled part of the *kuhoo* note. Subsequently, these notes

alternated with harmonically richer notes (presumed to be inspiratory by analogy with the preceding species), whose amplitude, frequency, and duration declined gradually. Brief soft broadband notes terminated the call. This was one of the most common calls. It was delivered mainly by males (Table 3) and sounded like "ahee...hew...KUHOO...kuru...kuru...kru...kru".

*Hoot* (II) (Fig. 3C–E; Tables 1, 2). This call began with fairly brief (50–100 msec), repeated, broadband notes (frequency descending;  $F_1$  was dominant), which increased successively in amplitude and rate of delivery. Intervening tonal sounds were evident between some of these notes (Fig. 3C, D). Terminal notes resembled introductory notes. The introductory notes were followed by the distinctive note type (nt-V, Fig. 3D) for which we named this call. This call was long (median duration ~7 sec), noisy, and with much energy in the lowest few harmonics. The carrier frequency ( $F_0$  ~650 Hz) decreased over note type V and expressed some rhythmic FM (Fig. 3D). This note grades into closely grouped notes in the example, then single notes, identical to those in the *Cackle* (Fig. 3F, G). *Hoots* were given mostly from crevices, especially just after peak colony activity in midday (Table 3). They sounded like "kuhoo... hooo... ooo...".

*Cackle* (III) (Fig. 3F, G; Tables 1, 2). This call consisted of a rapid rhythmic series of frequency-descending notes (inter-note intervals ~100 msec) of two distinct alternating types. One type (the first note, Fig. 3F) began with an apparent  $F_0$  at ~3 kHz (note type II; Table 1), but this presumably resulted from harmonic suppression, because about halfway through the note, it switched to about half that value (hence the appearance of greater harmonic richness in the second part of the note). The other note type was noisier. *Cackle* calls were given as series of staccato metallic-sounding notes, frequently performed as a loud duet by pairs (Table 3). The call sounded like "kut-tee...kut-tee... kre- kre- kree...".

*Whine* (IV) (Fig. 3H, I). The *Whine* was the species' longest call. It was similar to the *Hoot* in several ways and the two call types may intergrade. The *Whine* began and ended with brief broadband frequency-descending notes resembling *Cackle*; it varied greatly in duration (4–21 sec). Low-frequency tonal sounds (*t*), as in *Hoot*, occurred between many of the introductory notes (2 are marked, Fig. 3I). The most prominent (and loudest) part of the *Whine* was a repeated



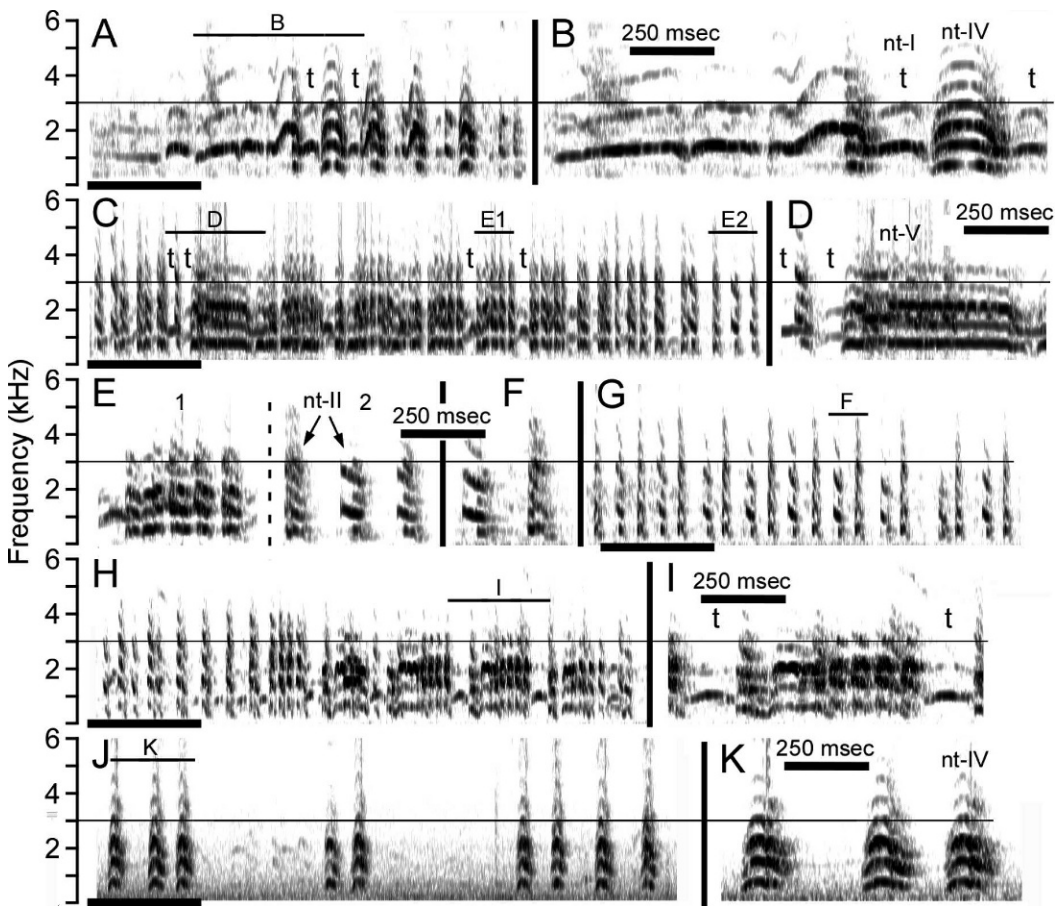


FIG. 3. Calls of Crested Auklet. (A) *Trumpet*. Two intervening tonal parts (t) are marked. (B) Part of panel (A) on different time scale. Some note types (nt-) are marked. (C) *Hoot*. (D) (E) Parts of panel (C) on different time scale. (F) Part of panel (G) on different time scale. (G) *Cackle*. (H) *Whine*. (I) Part of panel (H) on different time scale. (J) *Bark*. (K) Part of panel (J) on different time scale. All time scales are 1.0 sec, except as marked. The 3-kHz line is a visual guide.

compound note alternating with brief low-frequency ( $\sim 1$  kHz), harmonically weak, tonal sounds. It was delivered as a contact call from boulders and from within breeding crevices (Table 3). The call sounded like “*keew... keew...*”.

*Bark* (V) (Fig. 3J, K; Tables 1, 2). This was the most common and simplest call type. It consisted of long series of broadband, harmonically structured notes (each 200–400 msec long; Tables 1, 2), arranged in bouts of one to several notes. Successive bouts of three, two, and four notes are apparent (Fig. 3J). They were harmonically similar to but briefer than the harmonically rich notes in the *Trumpet* call (Fig. 3B). Both males and

females uttered this call at the colony and at sea (Table 3). It sounded like the yap of a small dog.

*Whiskered Auklet*.—We recognized five call types for this species (Table 2). They were based on a ground plan of harmonically rich, noise-free notes, lack of rapid pulsing or pulsed trills with some rhythmic FM, and with unremarkable frequency shifts. Harmonic suppression was apparent in many calls. Whiskered Auklet calls sounded high-pitched compared with those of other species, except Least Auklet. There was no suggestion of alternating inspiratory and expiratory vocal phases, unlike the preceding three species. Call duration was similar to that of Crested Auklets (range = 1–13 sec; means = 1–6 sec).

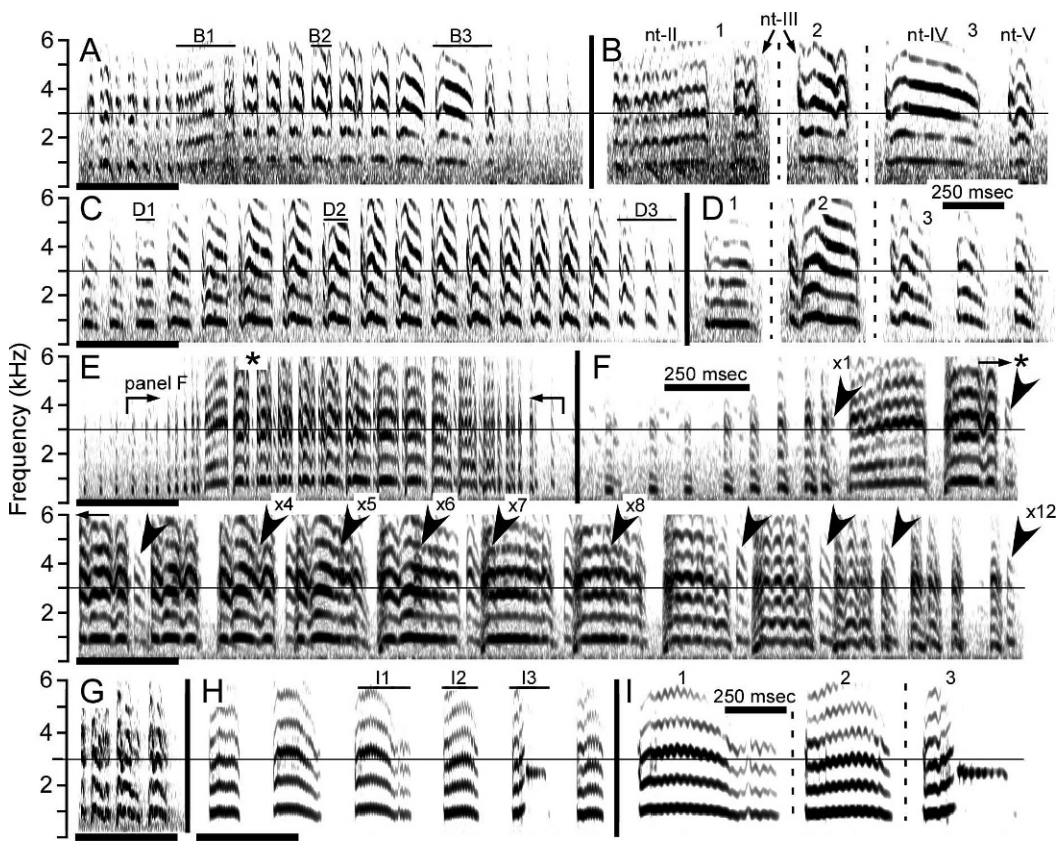


FIG. 4. Calls of Whiskered Auklet. (A) *Staccato Beedoo*. (B) Parts of panel (A) on different time scale; some note types (nt-) are marked. (C) *Metallic Beedoo* (some introductory and terminal notes are omitted). (D) Parts of panel (C) on different time scale. (E) *Duet Beedoo*. Segment between arrows is also shown in panel (F) (asterisk denotes break point on right side of following panel). (F) *Duet Beedoo* from panel (E) on different time scale with one bird's soft calls marked. (G) *Bark*. (H) *Mew* (6 examples). (I) Parts of panel (H) on different time scale. Time markers are 1.0 sec, except as marked. The 3-kHz line is a visual guide.

*Staccato Beedoo* (I) (Fig. 4A, B; Tables 1, 2). This call contained several note types (Table 2). We distinguish the *Staccato Beedoo* from *Metallic Beedoo* on the basis of whether the distinctive resonant *kirree* note (note type II; Table 1, Fig. 4B) was present. This call was a series of simple introductory notes (mainly frequency descending; Fig. 1A), followed by *kirree* (Fig. 4B 1). Rhythmic FM (at  $\sim 30$  Hz in the example) on a gradually rising carrier frequency was expressed throughout the note. This was followed by a graded series of harmonically rich notes that lengthened successively (to  $\sim 380$  msec: note type IV; Fig. 4B); some modulations of the carrier frequency were apparent. Several brief pulses ended the call. The dominant frequency was  $F_2$  or  $F_3$  in most notes. This was the most common

vocalization. It was given as an advertisement display throughout the night, especially during times of peak activity at the colony (Table 3).

*Metallic Beedoo* (II) (Fig. 4C, D; Tables 1, 2). This call type was a long ( $\sim 12$  sec) graded trill with undifferentiated parts. It began with brief (to  $\sim 70$  msec) notes (Fig. 4C) in which frequency descends slightly (note type I; Tables 1, 2). Note duration in this example increased progressively ( $< 90$  msec for the first 2 sec,  $\sim 120$  msec at 2.2 sec, and  $\sim 330$  msec at 4 sec) and then declined; terminal notes were identical to introductory notes. Note complexity changed in parallel: notes begin with a frequency drop followed by a rise, which became more pronounced (e.g., Fig. 4D 2) as calls increased progressively in duration, amplitude, and frequen-

cy.  $F_0$  was  $\sim 800$  Hz in introductory and terminal notes, and reached  $\sim 1.2$  kHz in the middle of the call. Dominant frequency of harmonics usually was  $F_1$  or  $F_2$  and, at times, changed within calls (e.g., Fig. 4D 2). This call was uttered predominantly in the colony before dawn (Table 3).

*Duet Beedoo* (III) (Fig. 4E, F; Tables 1, 2). This call consisted of several note types. All were strongly harmonic; long notes exhibited much FM. One bird in the example began the call with  $\sim 12$  brief ( $\sim 35$  msec) notes (note type I; Table 1), followed by a graded series of long ( $\sim 240$  msec) notes (note type II). Some of these notes gradually increased or decreased in carrier frequency, and had rapid rhythmic FM; others had frequency inflections. One bird in the example uttered soft, brief, frequency-descending calls, beginning about 1.5 sec after the first bird started calling (marked in Fig. 4F); the second bird's calls continued after the first had finished. Both birds (presumably mates) in many examples uttered series of loud calls simultaneously. This call was performed mostly as a duet from inside crevices (e.g., after one mate entered the burrow while the other was present inside). It became increasingly common over the breeding season. The rhythmic FM in the *kirree* notes (note type II, Fig. 4B) imparted a rapid vibrant "kree... kree...kree..." quality to the display.

*Bark* (IV) (Fig. 4G; Tables 1, 2). This uncommon brief call was composed of several harmonically rich notes, marked by one to several frequency inflections. This tremulous-sounding display was delivered just before departure from crevices (Table 3); it sounded like the bark of a dog.

*Mew* (V) (Fig. 4H, I; Tables 1, 2). These calls were uttered singly, or in sequences of up to 10 repetitions. Rapid rhythmic FM was overlain on a carrier frequency that usually increased then decreased gradually. Some calls ended with a sudden frequency shift (e.g., Fig. 4I 3), a quality that was absent in other of this species' calls. *Mew* calls were given by single birds, duetting birds, and multiple birds in chorus, mainly as contact calls (Table 3). Sound quality varied from pulse-like single "kik", "mew", and tremulous "kreew", to nasal "ew".

*Least Auklet*.—Adults uttered four kinds of vocalization. They represented a variety of harsh, atonal, chattering, and chirp-like sounds. Notes were uttered more rapidly (Table 1), calls were higher in frequency, and calls were briefer (only 0–6 sec long; means =  $< 1$ –3 sec), than in other

species. Call diversity was high; subjectively, it was second to that of Crested Auklets. This species, like the Whiskered Auklet, possessed no apparent alternating inspiratory and expiratory vocalizations.

*Chatter* (I) (Fig. 5A, B; Tables 1, 2). This call was a graded series of high-frequency ( $F_0 \geq 3$  kHz), rhythmically repeated notes, lasting 2–6 sec. The notes exhibited rapid rhythmic FM at a rate of  $\sim 50$  Hz (Fig. 5B). This was the most common call type; it was given only by males, mainly as an advertisement display (Table 3). It sounded like "scht-tshhhht-tshhhh-tshhht-tshht...".

*Deep Chatter* (II) (Fig. 5C, D; Tables 1, 2). This call was the most structurally complex in the repertoire. It consisted of an introductory series of pulsed notes, each  $\sim 150$  msec; pulse-repetition rate within these notes was  $\sim 45$ –50 Hz. Broadband noise characterized each pulse within these notes and dominant frequencies were diffuse, but mainly were between 2 and 5 kHz. The introductory notes graded into a series of louder and more complex pulses. These were broadband but less noisy, and had a clear dominant frequency ( $\sim 5$  kHz in the middle of Fig. 5D 1, 2). FM rate within these notes was  $\sim 55$  Hz. The beginning and end of this second note (note-type IV) were noisy (at times tonal) and of high amplitude. Notes declined in frequency, duration, and amplitude towards the end of the call, and became noisier. This vocalization was delivered from a hunched posture, as an advertisement display, and during times of peak colony activity (Table 3). It sounded like "tchhht.tschhht.tschhht...".

*Chirp* (III) (Fig. 5E; Tables 1, 2). This relatively uncommon and brief call was a brief trill, often repeated several times at intervals of  $\sim 70$ –80 msec (similar to the *Bark* of Crested Auklets). The notes had strong harmonic structure to  $\sim 9$  kHz ( $F_0 \sim 3$  kHz). This call was delivered in the colony or as a flight call when birds departed the colony (Table 3). It sounded like "scht" or "scht...schüt".

*Chirr-buzz* (IV) (Fig. 5F; Tables 1, 2). This call was a brief, rapidly modulated (pulsed) call (duration 0.3–0.5 sec, FM  $\sim 65$  Hz). It was noisy but had clear harmonic structure ( $F_0 \sim 3.5$  kHz in examples) with carrier frequency descending or approximately constant throughout the call. This call was delivered in response to the approach of predators. It sounded as a rasping, descending "whissssst".

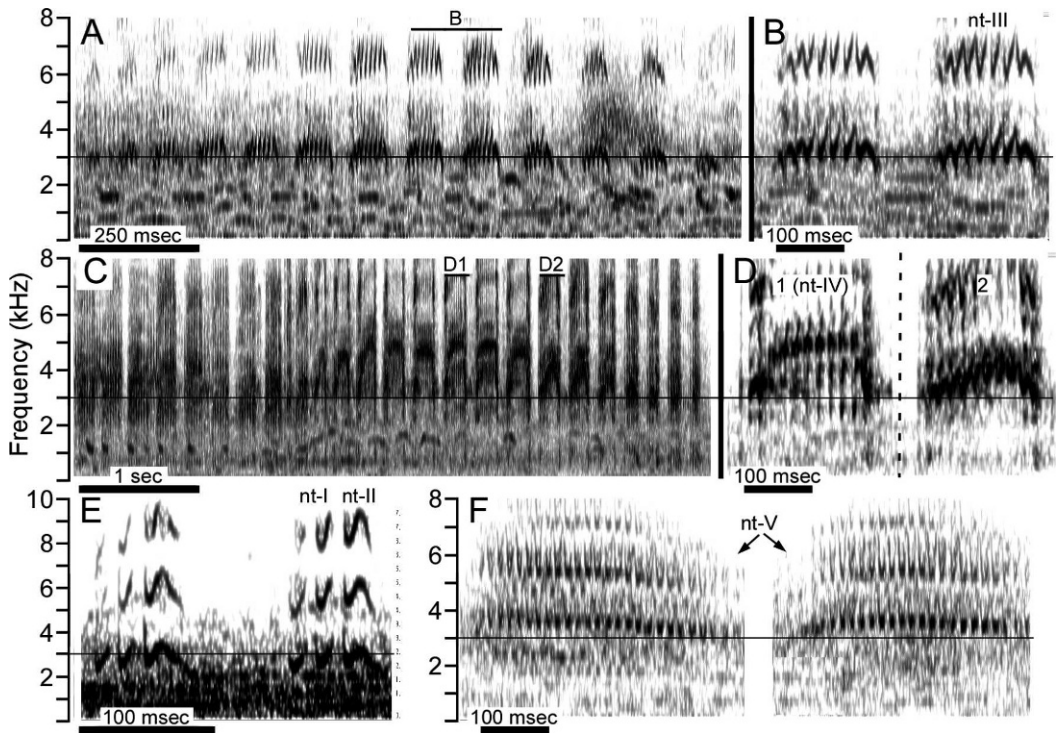


FIG. 5. Calls of Least Auklet. (A) *Chatter*. (B) Part of panel (A) on different time scale; some note types (nt-) are marked. (C) *Deep Chatter* (some introductory notes are omitted). (D) Part of panel (C) on different time scale. (E) *Chirp* (part of longer series). (F) *Chirr-buzz* (examples from 2 different birds). The 3-kHz line is a visual guide.

## DISCUSSION

Facial plumage and bills of breeding auklets are specialized as complex optical display structures (Jones 1999). We found comparable diversity and complexity in auklet vocalizations. Both optical and vocal displays are used extensively in sexual and agonistic contexts, and likely have been shaped by social selection, including sexual selection. Sexually selected displays can evolve rapidly and can be particularly sensitive indicators of low-level divergence, such as between conspecific populations or related species. Display evolution may be more conservative than generally thought (Wenzel 1992), and vocal evolution in Charadriiformes is notably conservative (Miller 1996, Miller and Baker 2009). Thus, high-level relationships may be revealed through analysis of multiple displays.

*Repertoire Size and Composition.*—A descriptive catalog of display types may be a poor approximation to a species' functional repertoire, because variations within named display classes may serve different functions (Marler 1977,

Marler and Tenaza 1977, Hailman and Ficken 1996). Repertoire structure was similar across auklet species: the basic vocal units (i.e., note types) were arranged in configurations to form displays, and individual note types appeared alone or in different display classes. We conservatively recognized 22 classes of adult vocal displays (including 28 note types) across species. This was an underestimate because: we lacked recordings from outside the breeding season and outside the breeding colony; chick and fledgling vocalizations were not sampled; we could not confirm several previously described vocalizations (*Krick* and *Kreer* of Cassin's Auklet: [Thoresen 1964]; *Chuckling* and *Soft-lure* of Least Auklet: [Jones 1993b]); and we considered repetitions of single note types to constitute displays.

Structural discontinuities between notes, recurring associations of different note types, and non-random ordering of and changes in note types within displays ("syntax"; Hailman et al. 1985, Sung et al. 2005), enabled recognition of acoustic classes in all species. Number of note types (4–9)

and repertoire size (3–5 display classes) were similar across species. Whiskered Auklet vocalizations were most diverse with nine note types and five display types. Qualitatively, vocal structure included pure-tones, pulses, rapid frequency modulations, broadband noise, smoothly rising and declining frequencies, and abrupt changes in frequency. Acoustic structure also varied in quantitative terms and was partly related to body size. For example, note duration ranged from 15 to 370 msec for Least Auklets and 45–1,250 msec for Parakeet Auklets; display duration ranged from 1 to 3 sec for Least Auklets and 4–19 sec for Cassin's Auklets; and inter-note intervals ranged from 2 msec for Least Auklets, to 1,010 msec for Parakeet Auklets. Brief, rapidly repeated notes characterized the smallest species. Frequency attributes varied even more, and reflected body size more closely, as in some other groups (Ryan and Brenowitz 1985, Bretagnolle 1996, Badyaev and Leaf 1997, Bertelli and Tubaro 2002).

*Acoustic Relationships Among Auklets.*—Harmonic structure and FM were similar in repertoires of Cassin's and Parakeet auklets. For example; Cassin's Auklet's *Krreerr-er* was structurally similar to *Raft Whinny* of Parakeet Auklets. The latter species' *Chip* call consisted of an arrangement of short pulses similar to the "kut-kut" segments of Cassin's Auklet's *Kut-I-eer*. Parakeet Auklet's *Whinny* was similar to *Kut-I-eer* of Cassin's Auklets, and its *Short Whinny* was similar to the *Kreerr-er* of Cassin's Auklets. The structure and FM of Crested Auklet notes and note-type composition in displays were most like those of Whiskered Auklets, but  $F_{\mu}$  was in lower harmonics in the former species. However, in *Trumpet*, note types *a* and *d* were arranged alternately and repetitively, as in Parakeet and Cassin's auklets. Whiskered Auklet displays were similar to those of Least Auklets in the predominant use of brief high-frequency notes, and the presence of sequentially graded note types over the display. The latter species' *Deep Chatter* was structurally analogous to the Cassin's Auklet *Kut-reeah* (Fig. 1C). *Chirr-buzz* differed from all other displays, but was spectrographically similar to *Hoot* of Crested Auklets.

Auklet species align in two groups based on syntactical arrangement of note types: (1) alternate-note arrangement of Cassin's and Parakeet auklets, and (2) arrangement of sequentially graded note types over the display of Whiskered

and Least auklets. The alternate arrangement of notes occurred in synchrony with a rhythmic, slow rocking of the head, and might correspond to alternating inhalation and exhalation. The vocalizing bird in group (2) species moves the head rapidly and asynchronously with respect to the temporal patterning of notes. Crested Auklets were mainly in group (2); however, this species lacked rapid head movements. Two note types (*a* and *d*) were arranged alternately in *Trumpet* and differed in  $F_{\mu}$ , which is characteristic of group (1). The *Trumpet* of Crested Auklets was unique among auklet vocal displays, for its accompanying postural display included ventral distension of the throat in the esophageal region.

Repertoires of Cassin's and Parakeet auklets were most similar to one another in alternate and repeated arrangement of several notes, presence of broadband noise, contrasting harmonic and frequency differences between note types, prevalence of brief pulses, and duetting. *Kut-i-eer* and *Kreerr-er* displays of Cassin's Auklets are likely homologous to *Whinny* and *Raft Whinny* of Parakeet Auklets (respectively), even though they occurred in different contexts. Introductions of some *Kut-i-eer* calls of Cassin's Auklet were long and had brief pulses, and resembled *Chip* of Parakeet Auklets. Crested, Least, and Whiskered auklet repertoires were characterized by sequential gradation in note complexity, predominant expression of trills, and absence of broadband noise. Notes of Whiskered and Crested auklets were similar. The Least Auklet repertoire was most similar to that of the Whiskered Auklet. This vocal comparison suggests that relationships might be closer than currently recognized between Cassin's and Parakeet auklets, and Whiskered and Crested auklets. The latter two species also have similar forehead crests and plumage odor (Byrd and Williams 1993, Jones 1993a).

*Acoustic Relationships of Auklets with Other Alcids.*—Six alcid clades are currently recognized: Alcini (murrets and allies); Cephini (guillemots); Brachyramphini (brachyramphine murrelets); Synthliboramphini (synthliboramphine murrelets); Fraterculini (puffins plus Rhinoceros Auklet [*Cerorhinca monocerata*]); and Aethiini. Recent molecular studies have clarified previously uncertain relationships (Strauch 1985, Mowm et al. 1994) of Aethiini within the family. The Alcidae arose in the early Paleocene and, soon thereafter (>50 Mya), split into two branches, one containing Fraterculini plus Aethiini (Friesen et. al 1996,

Thomas et al. 2004, Pereira and Baker 2008). These two highly ornamented clades diverged from one another ~50 Mya, so are both ancient in their own right. Cassin's Auklet is the oldest species in the Aethiini, having diverged from other auklets >20 Mya, and Least Auklet branched off next >15 Mya; relationships among the remaining species have not been resolved.

Compared with Aethiini, *Fratercula* species utter mainly soft single calls with simple FM; the *Multinote Call* of Horned (*F. corniculata*) and Tufted (*F. cirrhata*) puffins seems to be the only compound call (Cramp 1989; Lowther et al. 2002; Piatt and Kitaysky 2002a, b). The Rhinoceros Auklet is the most primitive fraterculine, having diverged from the *Fratercula* lineage nearly 30 Mya (Pereira and Baker 2008). Its calls and call repertoire are the most complex within the Fraterculini (Gaston and Dechesne 1996). This suggests the calls of *Fratercula* represent a derived state, and the common ancestor of Aethiini plus Fraterculini had complex calls and call repertoires, as do extant Aethiini and Rhinoceros Auklets. No obvious vocal homologies are shared by these latter two taxa, but Rhinoceros Auklets may possess one vocal display (*Mooring* with *Chucks*) characterized by alternating exhalant and inhalant sounds similar to some Aethiini (Gaston and Dechesne 1996). This structural arrangement, if it is homologous, would have originated at least 50 Mya, when the Aethiini-Fraterculini clade originated (Pereira and Baker 2008).

Repertoires of more distantly related alcids have few vocal similarities with auklets. Guillemot (*Cepphus*) vocalizations are mainly long, high-frequency, whistle-like notes, which are unique within the Alcidae (Nelson 1985, Butler and Buckley 2002). Murres (*Uria*) and Razorbill (*Alca torda*) (Alcini) mainly communicate over short distances with brief, low-frequency, guttural broadband growls (Cramp 1989, Gaston and Jones 1998, Lefevre et al. 2001); their calls are syntactically simple. The remaining member of this tribe (Dovekie, *Alle alle*) has complex calls and a large call repertoire and, like Aethiini, uses long-distance advertisement displays in the colony (Ferdinand 1969, Cramp 1989, Jones et al. 2002). Similarities between Aethiini and the Dovekie in call-note structure and arrangement are most parsimoniously explained by selection for structurally discrete call types for medium- to long-distance communication (Marler 1976).

More detailed acoustic descriptions may suggest some vocal similarities are homologous (Miller 1996); however, some non-sexually selected sounds (especially short range sounds), such as those used by chicks or alarmed adults, are more likely to reveal ancient homologies (Marler 1957).

*Environmental Selection on Vocalization; Potential Applications.*—We interpret transmission distance as an important selective pressure on vocalizations of Aethiini; another factor that may be important is light. Nocturnality makes optical communication difficult and many nocturnal species rely heavily on acoustic communication (e.g., Caprimulgiformes, Procellariiformes). Nocturnally active breeding alcids are Ancient Murrelet (*Synthliboramphus antiquus*; Jones et al. 1987, 1989), Xantus's Murrelet (*S. hypoleucus*; Drost and Lewis 1995), and Marbled Murrelet (*Brachyramphus marmoratus*; Nelson 1997, Dechesne 1998). We found no differences between nocturnal (Cassin's and Whiskered auklets) and diurnal auklets in repertoire size or vocal complexity.

Many seabird populations have declined or disappeared because of introduced predators, and the Aethiini are no exception (Gaston and Jones 1998). Seabird restoration efforts have included removing predators from islands, and enhancing recolonization through habitat restoration and call playback to attract prospecting birds (Kress 1997, Miskelly and Taylor 2004). Advertisement displays are adapted for long-distance transmission, and are audible over long distances (Wiley and Richards 1982, Endler 1993); some advertisement displays of breeding auklets at the colony site are candidates for playback efforts. Use of playback calls for nocturnal seabirds may be especially effective, because most species are highly vocal and use loud, long-distance calls in intraspecific communication (Bretagnolle 1996). This is likely to apply to nocturnal Cassin's and Whiskered auklets in Aethiini. Playback of *Kut-reeah*, *Staccato Beedoo*, and *Metallic Beedoo* may be useful for future island restoration programs. *Raft Whinny* and *Duet Whinny* calls of the diurnally active Parakeet Auklet may be useful in conditions of poor visibility (e.g., fog), which is prevalent in its breeding range.

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