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REPERTOIRE, STRUCTURE, AND INDIVIDUAL DISTINCTIVENESS OF THICK-BILLED MURRE CALLS[1]

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Abstract. We describe the vocal repertoires of Thick-billed Murre (*Uria lomvia*) adults and chicks during the breeding season. Using recordings from throughout the chick-rearing period, we identified four distinct calls of chicks and six of adults. We present sonograms and quantitative descriptions of each call and summarize the behavioral context in which they were used. Chick calls are mostly flute-like sounds at approximately the same pitch that tend to develop from a simple peep during hatching through a rapidly frequency-modulated departure call, given shortly before, during, and after they leave the colony at fledging. Departure calls appear to facilitate interactions between the chick and the attending male parent during this risky period for the chick. Adult calls are lower pitched and sound more gruff, with different call types having significantly different pitch, duration, and number of syllables. Among-individual variation in the crow calls of adults accounts for 44% of the measured variation in this call and indicates the potential for individual recognition, such as the recognition of parents' calls by their chicks, which we have previously documented. Temporal features may form the basis of recognition of adult calls in this species, given that they accounted for twice as much variation as frequency features among individual adults.

Key words: alcids, call structure, colonial, individual recognition, Thick-billed Murres, Uria lomvia, *vocal repertoire.*

INTRODUCTION

Most communication in dense bird colonies occurs over short distances, mainly between individuals such as mates or parents and young. Colonial birds must overcome two key difficulties with such communication: sending and receiving messages above the continuous background noise of similar calls, and recognizing individuals when so many are present (Falls 1982, Wiley and Richards 1982). These factors create risks, like misdirected parental care amid crowded nesting sites and offspring.

Vocalizations over short distances mainly serve to attract the receiver's attention and identify the signaler, so further communication with more subtle cues can begin (Wiley 1976). Colonial birds like penguins, gannets, gulls, and terns have adaptations that enable effective communication in noisy, dense environments (Falls 1982). For example, a limited repertoire and repetition can improve the detection of signals. Selection also favors sounds for optimum signal transmission in the bird's environment, so the physical structure of vocalizations may be adapted to noisy and call-degrading conditions (Morton 1975). Short-range calls in a dense colony should be selected for maximum individuality and ease of location. Wide-spectrum sounds with sharp changes in amplitude and limited frequency modulation are best for this purpose (Wiley and Richards 1982).

Vocalizations of non-passerine birds are mainly ''calls'' (short, simple sounds that tend to be given in specific contexts or behavior patterns and produced year round by both sexes), whereas passerines use both calls and ''songs,'' the more complex sounds typically given by males during the breeding season (Catchpole 1979). In general, calls have not been well studied compared to the extensive literature on passerine

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song (reviewed by Kroodsma and Miller 1982, Catchpole and Slater 1995).

We studied vocalizations of the Thick-billed Murre (*Uria lomvia*), a highly colonial seabird in the family Alcidae. Members of this holarctic species breed side-by-side on narrow rock ledges of steep coastal cliffs and offshore islands (Gaston and Jones 1998). Due to the high densities and large numbers of individuals present, a murre colony is a prime example of a noisy environment where short-distance communication predominates. Even though Thick-billed Murres also use distinctive visual signals for short-distance communication (Tschanz 1968), they use calls extensively and we expected that such calls would play an important role in individual recognition (Lefevre et al. 1998).

Our study had three objectives. First, we described the Thick-billed Murre vocal repertoire and its behavioral context to provide a basis for future studies of communication and coloniality in murres. Second, we defined quantitatively both the structure and individual distinctiveness (''individuality'') of calls to determine the potential physical basis for parent-offspring recognition that we have previously documented (Lefevre et al. 1998). Third, we assessed call structure in relation to presumed function and the acoustic environment in the colony.

METHODS

STUDY AREA

Our research was conducted at Coats Island, in northern Hudson Bay, Nunavut, Canada (62°30′N, 83°00′W) during the 1994 and 1995 breeding seasons. An estimated 30,000 pairs of Thick-billed Murres breed on 75-m high cliffs at this relatively small colony, in two subsections about 1.5 km apart along the northeast side of the island. We worked at the western subcolony of approximately 15,000 breeding pairs that has been the subject of a long-term demographic study (Gaston et al. 1994).

VOCAL RECORDINGS

Observations of murre vocalizations were made in 1994, and calls were recorded from 28 June–18 August 1995. We obtained 36 hr of adult and chick recordings, including all stages of breeding after egg laying began. Recordings were obtained throughout the day, and in late evening during chick departures. We sampled the spontaneous calls of adult birds throughout the colony, many of which were individually banded from ongoing research. To enable estimates of individual variation, we recorded banded adults where possible.

To investigate the ontogeny of chick calls, we recorded banded chicks of a known age from one area of the colony (area Z; Gaston et al. 1994). We attempted to record a bout of at least three calls from the same chick during three stages of development, based on approximate hatch dates (± 2 days), feather development, and degree of chick mobility (Tuck 1961). Chicks were downy and stationary in the ''early'' stage (from pipped eggs to about 5 days old), downy and mobile in the ''middle'' stage (about 6–13 days old), and had no down and were approaching departure age in the ''late'' stage of development (≥14 days old). Each chick was lifted from its site so we could record calls of adequate amplitude without background noise. These calls sounded similar to unstimulated chick calls throughout the colony but we cannot make a quantitative comparison because of the difficulty of obtaining clear recordings of unstimulated calls. Chick calls were recorded in the open with the microphone about 1 m from the chick.

Recordings were made with WM-D6 Sony Walkman Professional cassette recorders using an Audio-Technica directional microphone (model AT815a). Recordings of clear calls with minimum background noise were digitized on computer using the program Canary 1.2 (Cornell Laboratory of Ornithology 1995). Sound spectrograms were produced with a 175-Hz filter.

To compile the vocal repertoire, we classified calls both by ear and using spectrograms (based on number of syllables, duration, and changes in frequency—increasing or decreasing). We observed murres from blinds throughout the season to determine the array of behaviors associated with each call from adults and older (middle and late stage) chicks. We could not determine the context of early-stage chick-calls because the sources of their soft sounds were difficult to locate and brooded chicks were not visible. For consistency, we used pre-existing call names where possible; names that we applied ourselves were based on renditions of sound rather than apparent function. However, we retained the name ''departure call'' as it is well established and intimately associated with chick departures.

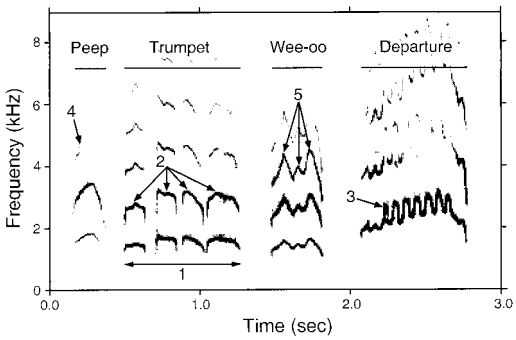

FIGURE 1. Sound spectrograms of the call repertoire of Thick-billed Murre chicks at Coats Island, Nunavut, showing variables measured on each call: (1) duration (sec), (2) number of syllables, (3) frequency at maximum amplitude (kHz), (4) maximum frequency (kHz), and (5) number of frequency peaks. The progression of calls from left to right represents the general ontogeny of chick vocalizations, from the pipped egg stage to fledging/colony departure at about 20 days of age.

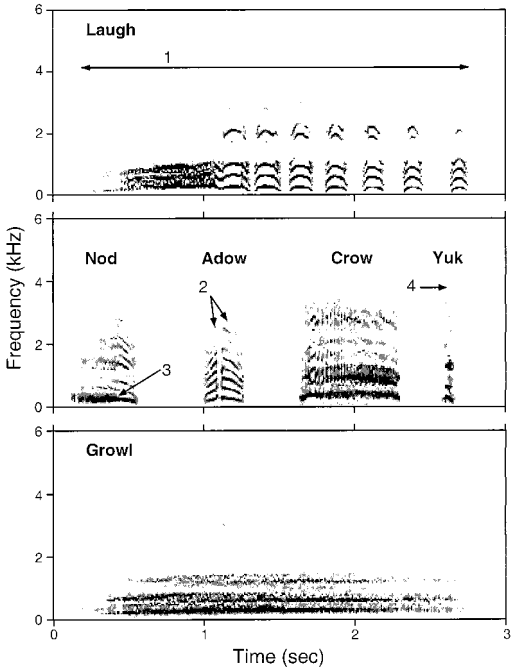

FIGURE 2. Sound spectrograms of the call repertoire of adult Thick-billed Murres during the breeding season at Coats Island, Nunavut, showing variables measured on each call: (1) duration (sec), (2) number of syllables, (3) frequency at maximum amplitude (kHz), and (4) maximum frequency (kHz).

STATISTICAL ANALYSIS

For each call type, we analyzed every third call from our sample of clear recordings, until a sample size of 25 calls was obtained or all available calls were used. From spectrograms we measured the number of syllables, duration (sec), frequency at maximum amplitude (FMA), and maximum frequency (kHz) of both chick and adult calls. All measurements were calculated by Canary. Some chick calls had clear frequency peaks that we also counted (variables shown in Fig. 1 and 2).

To examine the individuality of adult calls, we measured the number of syllables, call duration, and frequency (minimum and maximum frequencies, FMA, and FMA of fundamental frequency) of the crow calls of 10 marked individuals. We used 3–5 calls from each of 2–3 distinct calling ''bouts'' per adult, defined as periods of calling separated by $\geq$5 min (three calls bout^{-1} if three bouts sampled, five calls bout^{-1} if two bouts sampled). We quantified variance due to individual and bout effects using repeated measures ANOVA. We analyzed the crow call because mates used this call in communication, and chicks responded when their parents used this call on ledges (e.g., during feedings). Hence, this call appeared to be the most likely to be used for parent-offspring recognition (Lefevre et al. 1998).

In all analyses we checked for normality and homogeneity of variances and applied transformations when necessary to meet these assumptions in ANOVA.

RESULTS

CHICK REPERTOIRE

Vocalizations of Thick-billed Murre chicks were flute-like, shrill, frequency-modulated squeals, shorter and lower in amplitude than adult calls. As chicks became older, their calls grew louder.

We identified four distinct chick vocalizations (Fig. 1), which differed significantly in number of syllables, number of frequency peaks, and duration, but not in FMA (Table 1). All chick call types consisted of harmonics. The mean frequency range of the four call types was 7.0 kHz and the average minimum range across all call types was 5.8 kHz. Compared to a minimum criterion of 3 kHz for ''wide frequency range'' (Ficken and Popp 1996), these were clearly wide-band sounds. The following easily distinguishable call types represent all those we encountered in the chick vocal repertoire. Each call type was heard from each age group at least oc-

TABLE 1. Temporal and frequency characteristics of the calls of Thick-billed Murre chicks. Values are mean ± SE. Sample sizes refer to number of chicks measured; one call per individual was analyzed. ANOVA statistics comparing characteristics across call types are shown at bottom of table.

Call type	*n*	Syllables	Peaks	Duration (sec)	FMA[a] (kHz)
Peep	15	1.0 ± 0.0	1.3 ± 0.2	0.26 ± 0.02	2.66 ± 0.22
Trumpet	10	3.2 ± 0.1	2.2 ± 0.5	0.68 ± 0.04	2.38 ± 0.23
Wee-oo	20	1.0 ± 0.0	1.9 ± 0.3	0.58 ± 0.06	2.50 ± 0.16
Departure	20	1.1 ± 0.04	5.9 ± 0.6	0.45 ± 0.13	2.51 ± 0.12
$F_{3, 61}$		321.4	23.2	13.3	0.3
P		< 0.001	0.001	0.001	0.81

[a] Frequency at maximum amplitude.

casionally, except the departure call, which was not heard from early chicks.

Peep. The peep was a simple, short, one-syllable sound of low amplitude. Peeps were typically heard from pipped eggs (during hatching) until the early stage of development, but middle and late-age chicks also gave a similar one-syllable call of higher amplitude.

Trumpet. Chicks gave the 3–4 syllable trumpet call frequently from hatching (pipped egg) until the early stage of development, and infrequently during the middle and late stages. This call often increased in amplitude on the final syllable and can be described phonetically as ''bah-bah-BAH.''

Wee-oo. This call was similar to the trumpet, but with only one syllable. The call ascended in frequency at the start, descended at the end, and contained an average of two frequency peaks. Phonetically the call sounds like ''wee-oo''. The ''wee-oo'' call was soft and tentative in young chicks but was given insistently and repeatedly by middle-aged chicks. The ''wee-oo'' call appears to form the basis of the more complex departure call of older chicks and was also given by them. Chicks used this call in interactions with parents (e.g., when a fish was brought to the chick), or during times of distress (e.g., during observer or predator intrusion).

Departure call. Departure calls were loud and piercing. This rapid frequency-modulated call, typical of late-stage chicks, appeared in sound spectrograms as one syllable with an average of six frequency peaks (Fig. 1). Although this syllable was often emitted one at a time by a chick, it also was frequently emitted in pairs, and is thus sometimes referred to as a two-syllable call (described as ''piu-piu'' by Gaston and Nettleship 1981). This call ascended in frequency at the start and descended at the end, similar to the ''wee-oo'' call. A comparison of sonograms from different chicks indicated that departure calls can be individually distinct (see Fig. 1 in Lefevre et al. 1998), but we did not record enough of these calls from each chick to permit quantitative analysis of within and between-individual variation.

Chicks began to use the departure call in the middle stage of development, but it was heard most frequently from late-stage chicks, particularly from 2–3 days prior to colony departure. In the hours immediately before departure, chicks continually used this call in apparent communication with their male parent, who departs with the chick when it is 3 weeks old (Harris and Birkhead 1985). Calling between parents and chicks often resulted in bill-touching and movements toward the edge of breeding ledges. Chicks continued to give this call on the ocean after fledging.

ADULT REPERTOIRE

There was little resemblance between the calls of chicks and adults. Compared to the flute-like sounds of chicks, vocalizations of adult Thick-billed Murres sounded harsh and gruff. Adult calls were lower pitched and had a simpler structure with little if any frequency modulation. Most calls had harmonic structure, abrupt onsets and terminations, and repetition of syllables.

We identified six distinct call types (Fig. 2) and these differed significantly in number of syllables, duration, and FMA (Table 2). The mean frequency range of the six calls was 6.7 kHz, and the average minimum range among the types was 4.5 kHz. Like chick calls, those of adults were clearly wide-band sounds, and intermediate calls were sometimes heard. Adult murres used each call in a variety of behavioral situations (Table 3) and often combined them in

TABLE 2. Temporal and frequency characteristics of adult Thick-billed Murre calls. Values are mean ± SE. Sample sizes refer to number of adults; one call per individual was analyzed. ANOVA statistics comparing characteristics across call types are shown at bottom of table.

Call type	*n*	Syllables	Duration (sec)	FMA[a] (kHz)
Laugh	25	8.1 ± 0.6	2.18 ± 0.16	0.65 ± 0.14
Nod	25	1.0 ± 0	0.51 ± 0.03	0.32 ± 0.03
Adow	25	2.0 ± 0	0.28 ± 0.02	0.88 ± 0.15
Crow	73	1.1 ± 0.04	1.00 ± 0.03	0.92 ± 0.08
Yuk	4	1.0 ± 0	0.06 ± 0.01	0.49 ± 0.23
Growl	10	1.0 ± 0	2.48 ± 0.14	0.41 ± 0.05
$F_{5, 164}$		129.8	111.6	5.1
P		< 0.001	< 0.001	< 0.001

[a] Frequency at maximum amplitude of call.

vocal displays (descriptions below). Calls were typically used during interactions among murres on breeding ledges; birds flying above the colony made no vocalizations. We describe the following call types from our adult samples.

Laugh. This call, a long, drawn-out introductory syllable followed by a series of short, clipped syllables, is similar to the sound of a human laugh, and phonetically sounds like ''RAH-rah-rah-rah-rah-rah. . . .'' Laugh calls contained an average of eight syllables which had a relatively constant frequency but decreased in amplitude and duration toward the end of the call. The laugh call likely has a social function as it was a common call, often heard throughout the colony in a loud, simultaneous chorus. It was contagious, spreading among ledges in a ripple effect when disturbances such as fighting occurred. Laugh calls were typically repeated several times by individuals, often triggered by ''nod'' calls from surrounding murres. Breeding adults bent their heads down low and often toward their undersides when ''laughing,'' but adults without eggs or chicks also gave this call.

Nod. The low-pitched, one-syllable nod call dropped off in frequency toward the end. The name (Tschanz 1968) refers to the distinctive ''nodding'' or bowing posture that accompanies the call; adults craned their necks downward and forward, sometimes bending their bodies so low that their beaks and/or undersides touched the ledge. This behavior and call were repeated many times for up to several minutes, and often a bird gave the call in pairs. Nod and laugh calls were regularly heard at the same time and the nod also was common and contagious, spreading throughout the colony during disturbances. Nod

TABLE 3. Behaviors associated with vocalizations of adult Thick-billed Murres at Coats Island, Nunavut, during the breeding season.

Behavioral context	Call type[a]				
	L	N	A	C	G
Interactions between mates					
Greeting/arrival at breeding site	S		S	T	
Copulation:					
Male	T			T	
Female			T		
Mutual preening	T			S	
Change-over on egg/chick				T	
Interactions between parents and young					
Return to egg after absence			S	T	
Mate brings fish for chick	S			T	
Calling to chick (e.g., after disturbance)				T	
Departure from colony				T	
Other contexts					
Fights	T	T	S	T	
Predator/human observer nearby	T	T	S	T	
Conspecific intrusion on ledge	T	T		S	
After chick is fed nearby	T	S		S	
Murre resting alone at nest site					S
Murre covered in mosquitoes				S	

[a] L = laugh, N = nod, A = adow, C = crow, G = growl. Frequency of occurrence in stated context during this study: T = typically, S = sometimes, blank = never.

calls seemed to occur only during periods of ''uneasiness'' such as during intrusions by conspecifics, predators, or human observers. Murres with or without eggs gave this call.

Adow. This two-syllable call was rapid compared to other calls and often higher pitched (Table 2). There was a brief pause between the first syllable, which ascended in frequency, and the second, which descended (Fig. 2). This call had two distinct variations; stress was placed usually on the second syllable (''a-DOW'') but sometimes on the first syllable (''GECK-o''). This call was used in a variety of contexts (Table 3).

Crow. The crow call was typically a one-syllable call, ascending then descending in frequency and longer than the other calls. The ascending portion is similar to the first syllable of the laugh call. The crow calls of some adults had a brief but distinct pause in the middle of the call, creating two syllables. Phonetically the call sounded like ''ARR-ahhh,'' often repeated several times. It was high-pitched compared to other calls (Table 2) and frequently had a harsh, raucous quality. This call was used in many different interactions between mates or between parents and young (Table 3). Crow calls given in different contexts were not sufficiently distinct in either duration (ANOVA, $F_{7,66} = 1.9$, $P = 0.08$) or FMA ($F_{7,65} = 1.1$, $P = 0.36$) to justify describing them as separate calls. However, those given by mates during changeovers at breeding sites were particularly distinct. For example, when eggs or young chicks were present, an incoming mate always gave one or more crow calls before switching places with its incubating/brooding partner. These were harsher and louder than other crow calls and could be used to instantly locate a site where partners were switching off, a helpful technique for reading leg bands. Such calls were heard infrequently when chicks were older, suggesting that the call is a means of coordination between mates to avoid losing an egg or young chick from narrow ledges. During greetings, either the incoming mate, the site holder, or both mates gave crow calls, sometimes in combination with laugh and/or adow calls. Murres that landed at an empty site did not call. Crow calls used by parents in interactions with chicks sounded less harsh than those used in changeovers.

Yuk. This brief burst of sound, a very short syllable, is similar to a rapid human sneeze. The yuk call was heard infrequently and the context in which it was used is unknown.

Growl. The growl is a low-pitched, drawn-out call, with a mean duration of approximately 2.5 sec. Growl calls had a relatively constant frequency over time, but decreased in amplitude until barely audible. This call was never associated with interactions between murres. Adults who uttered this call appeared to be resting at their sites, ''sitting'' on the ledge with eyes partially shut, neck drawn in, and beak tilted upward.

VARIATION IN ADULT CROW CALLS

A comparison of sonograms from different adults indicated that calls are individually distinct (see Fig. 1 in Lefevre et al. 1998). Some variance in all measured characteristics was due to differences among individuals (range 10.7–90.4%), but duration, number of syllables, and maximum frequency were the only variables that were individually distinct (greater variance among individuals than within bouts of individuals, Table 4). Individual differences were the most important factor contributing to variation among crow calls, accounting for an average of 43.9% of the variance among all five measured characteristics; differences among bouts of individuals accounted for an average of 19.7% of the variance, whereas variation within bouts of individuals accounted for an average of 36.4%. Temporal characteristics were, on average, more than twice as individually distinct as frequency characteristics, with among-individual variation accounting for 69.1% of the variance of duration and number of syllables combined, but only averaged 27.1% of the variance of maximum frequency, call FMA, and fundamental frequency FMA combined (Table 4).

DISCUSSION

VOCAL REPERTOIRES

We identified four chick calls (Fig. 1) and six adult calls (Fig. 2) in the vocal repertoire of the Thick-billed Murre during the breeding season. We could not study the calls of immature birds because Thick-billed Murres do not return to the colony for at least two years after departure (Gaston et al. 1994). Thus we cannot comment on the transition between chick and adult calls. The development of a chick's vocal repertoire generally proceeds from short, soft, simple sounds with little frequency modulation (peep

TABLE 4. Repeated-measures ANOVA statistics for temporal and frequency characteristics of Thick-billed Murre crow calls at Coats Island, Nunavut, compared within and between individuals. Two or three calls of the same 10 adults were measured during each of two or three recording bouts.

Characteristic	Effects of				Percent of variance due to		
	Individuals		Bouts				
	$F_{9, 60}$	P	$F_{17, 60}$	P	ID[a]	Bouts	Error[b]
Duration (sec)	6.5	<0.001	1.7	0.07	47.7	9.7	42.6
No. syllables	73.2	<0.001	1.2	0.31	90.4	0.5	9.1
Max frequency (kHz)	6.6	<0.001	2.1	0.02	51.1	12.5	36.4
Call FMA[c] (kHz)	1.4	0.25	5.8	<0.001	10.7	54.0	35.3
FF FMA[d] (kHz)	2.3	0.07	2.2	0.02	19.5	21.7	58.8

[a] Individual identity.
[b] Within-individual variation.
[c] Frequency at maximum amplitude of call.
[d] Frequency at maximum amplitude of fundamental frequency.

call) to loud, shrill calls that are longer, more complex, and have rapid frequency modulation (departure call). The calls of adult murres, low-pitched, harsh sounds with little frequency modulation, are strikingly different from those of chicks. Besides the constraint of small body size, chicks may have high-pitched, frequency-modulated calls because they are more effective on the ocean, where the low-pitched sounds of the ocean would tend to mask low-pitched calls. After chicks jump from their cliff ledges during colony departure, these calls play a key role in the reunification of separated parents and chicks (Gilchrist and Gaston 1997).

In Table 5, we compare our findings to previous descriptions of Thick-billed Murre calls. Other authors have described a total of three chick calls and eight adult calls for this species (Cramp 1985), similar to our findings. Any discrepancies from earlier descriptions may relate to differences in the approach to call definition. Some earlier writers, for example, have used both context and apparent function to define call types, whereas we defined separate calls strictly by discontinuities in their sounds. For example, we consider the ''male copulation call'' and the ''leap call'' (given by parents at departure), described separately by Cramp (1985), as contextual variations of the crow call, because they do not differ significantly in structure from other forms of crowing. However, crow calls during incubation changeovers sounded distinct from other forms, and the difference in durations of crow calls given in different contexts was almost

TABLE 5. Names given to Thick-billed Murre calls by previous authors.

Call type	Previous names[a] (based on Cramp 1985)
Chick calls	
Peep	''fretful cheep'' (1)
Trumpet	not described
Wee-oo	''wee-oo, wee-oo'' (1); food call (2)
Departure	''weee-weee-weee'' (1); ''piu-piu'' (3)
Adult calls	
Laugh	laughing (3); hawing call (4); ''rrr-haw-haw-haw-haw'' (2)
Nodding	alarm-bowing call (2); nodding call (5)
Adow	uggah-call (6); ''owka'' (1); ''uggah'' (2); ''cu-cauk'' (3); ''ger-ou,'' ''jer-ow'' (4)
Crow	several variations of cawing and/or crowing, luring call, greeting call (5); ''arrr'' (3); male copulation call (6)
Growl	contentment call, satisfaction call (5); ''grrr'' (2)
Yuk	not previously described

[a] Previous call names and phonetic descriptions (in quotes) from: (1) Tuck 1961; (2) Pennycuick 1956; (3) Gaston and Nettleship 1981; (4) Williams 1972, cited in Cramp 1985; (5) Tschanz 1968 (Common Murres); (6) Cramp 1985.

significant ($P = 0.08$). A more detailed analysis might reveal differences that would justify classifying some forms of crowing as separate calls.

Studies of other colonial alcids have reported similar, or larger, adult repertoires than we describe for Thick-billed Murres, but differences in call definition complicate any interspecific comparison of call types. Variation in sampling methods, timing of the study, and categorization of call types allows for only crude comparisons. For example, the fact that we found fewer calls for Thick-billed Murres than Tschantz (1968) found for Common Murres (*Uria aalge*) may be due to an under-representation of call types in our sample of recordings. However, despite these constraints, the question of differences in repertoire size and complexity among alcids remains an interesting one. In particular, more information about the vocalizations of nocturnal alcids and/or solitary-nesting alcids would allow for better comparison among species, and would shed more light on the ecological factors contributing to the evolution of vocalizations in this family.

CALL STRUCTURE

In some ways, the calls of Thick-billed Murre chicks appear ill suited for communicating in a noisy colony. Their low intensity and high frequency, typical of parent-offspring communication, make them harder to hear, but they have other structural features that make them maximally locatable. All four chick calls are wide-band sounds with sudden onsets and endings. This pronounced amplitude modulation allows the receiver to detect differences in the arrival time or pressure of sound waves at each ear and thus to better locate their source (Catchpole 1979). Although chick calls have a relatively high frequency, sound attenuation should not be great over the typically short distances between parents and offspring.

Adult murre calls also have features that enhance detection. Wide-band sounds and lack of frequency modulation make them easy to detect and, as with chick calls, their sudden starts and stops make them easy to locate. One exception is the growl, a long, soft call that begins and ends gradually. This was the only call used by solitary, resting murres and hence did not appear to be used in communication among birds.

Another predominant feature of murre calls is repetition. Crow calls were repeated about three times during a vocal display, and adow calls were repeated about four times. Such redundancy also facilitates communication in a bedlam of noise.

Murre calls are strikingly similar to those of penguins in many ways. Although not closely related, alcids and penguins are ecological counterparts in different hemispheres. Penguin calls comprise repetitions of short sounds with wide frequency ranges and sudden starts and stops, similar to murre calls. Such convergence in vocal structure also is found in other diverse animal taxa—colonial birds, seals, amphibians, and insects have all evolved repetitive calls with abrupt syllables to maximize their detection in high-density situations (Jouventin 1982).

INDIVIDUAL DISTINCTIVENESS OF CALLS

Adult calls were quite distinctive among individuals with 43.3% of variance in crow calls due to differences among individuals. We previously determined experimentally that chicks as young as 3 days old could distinguish between the calls of their parents and both stranger and familiar murres in this colony (Lefevre et al. 1998). Thus, there is clearly the potential for individual recognition on the basis of calls.

We also found that murre parents can identify calls of their own chicks during the late stage of development (Lefevre et al. 1998), and it would be useful to test whether adults can also recognize the calls of very young chicks. Based on the results of cross-fostering experiments (Lefevre et al. 1998), we expect the calls of very young chicks to be more difficult to recognize.

Studies of vocal features suggest that relative structural variation can be used to predict which features of bird sounds are most important for individual recognition (Falls 1982). For adult calls, we found time features were more individually distinctive than frequency features (Table 4), suggesting they are likely an important cue for individual recognition. This is similar to findings for other seabirds (Tschanz 1968, Jouventin 1982), but opposite to passerines, where individual information appears to be encoded mainly in the frequency pattern of bird song (Brooks and Falls 1975, Fletcher and Smith 1978).

This difference between seabird and passerine vocalizations makes sense in view of the limits to sound propagation in different environments. On their breeding colonies, seabirds communi-

cate over short distances amid background noise, so their calls should be selected to be maximally locatable. This environment favors a wide-spectrum sound with sharp amplitude modulation and limited frequency modulation (Wiley and Richards 1982), where individuality may best be encoded in the temporal features of vocalizations. Conversely, passerines usually communicate over long distances, often in forests where sounds rapidly degrade due to reverberations. Tonal sounds with complex frequency modulation are best suited to these conditions, so frequency characteristics are most important for individual recognition (Wiley and Richards 1982). Further experiments with call manipulation could determine whether the predominance of temporal features in the among-individual variation that we documented in adult Thick-billed Murres is important in the actual process of vocal recognition in this species.

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