

THE VOCAL REPERTOIRE OF THE ANCIENT MURRELET

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Abstract. We investigated the vocalizations of the Ancient Murrelet (*Synthliboramphus antiquus*), a seabird of the North Pacific, to determine how the size and structure of their vocal repertoire relates to their nocturnal activity at breeding colonies. Nine distinct vocal displays were found, a repertoire of similar size to that of two other alcid species and several passerines. Most vocalizations consisted of broad band sounds with rapid frequency and amplitude modulation. The *chirrup call*, a short (0.5 sec) vocalization performed in many situations, did not differ in use or structure between the sexes. *Chirrups* had great individual stereotypy in structure, important in individual recognition of parents by young and possibly between mates. *Song*, a complex vocal display performed by males, was usually given from perches high in trees in the colony. *Song* may function in courtship and mate attraction, but apparently not for defense of long-lasting territories. Several *song* variants were recorded, at least one of which appeared to function as an agonistic signal to other males. Ancient Murrelet vocalizations have simple 'combinatorial' properties in that they consist of a few acoustic elements combined in various sequences to produce vocal displays with different functions. Although there was little evidence that the Ancient Murrelet repertoire was larger than those of other alcids, the vocalizations were structurally more complex and include the song-like male advertising display. This likely relates to the nocturnal timing of social behavior of this species, which must restrict the usefulness of visual displays. We conclude that Ancient Murrelet vocal signals exhibit a number of adaptations to the unusual habits of this nocturnal, forest-nesting seabird.

Key words: Ancient Murrelet; *Synthliboramphus antiquus*; vocal repertoire; vocalizations; seabirds; Alcidae.

INTRODUCTION

Seabirds that forage by day but visit their nest sites or colonies only at night include many species with conspicuous vocalizations used during their night-time activities. Many shearwaters and petrels, Procellariidae, storm-petrels, Hydrobatidae (Brooke 1978, Storey 1984, James 1985, James and Robertson 1985), and several species of auk, Alcidae, are active and vocal at their nesting colonies only at night. Vocalizations are assumed to take on greater significance than visual displays because of the low light levels in which much of these species' social behavior takes place (Brooke 1978). In this study we investigated the structure and use of vocalizations by the Ancient Murrelet (*Synthliboramphus anti-*

quus), a small, colonial, nocturnal alcid of the North Pacific.

Since Ancient Murrelets are active above ground at their colonies only during periods of nearly complete darkness (Sealy 1976, Jones 1985), we might expect to find that they have a vocal repertoire specially adapted for use in situations where visual communication is severely restricted. Ancient Murrelets have individually distinctive calls which form the basis for a system of mutual vocal recognition between parents and offspring which is used during the nocturnal departure of family groups from the colony (Jones et al. 1987a). Other studies (e.g., Beecher 1981, Jouventin 1982, etc.) have shown that the calls of colonial species are more complex and individually identifiable than those of related solitary nesting species. In this study we classified the vocal repertoire into discrete displays based on structure, to test the hypothesis that the nocturnal and colonial lifestyle of Ancient Murrelets has resulted in a specialized repertoire (i.e., more

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complex or with a larger number of displays) compared to the vocalizations of the diurnal alcids. Further, we addressed the question of whether murrelet vocalizations are 'combinatorial' (i.e., the repertoire consists of rearrangeable elements that have different meanings when presented in different sequences [Wilson 1975]), a form of repertoire organization that has been described for only a few vertebrates other than humans (e.g., Black-capped Chickadee *Parus atricapillus*, Hailman and Ficken 1986; Laughing Gulls *Larus atricilla*, Beer 1976; and cotton-topped tamarin *Saguinus oedipus*, Cleveland and Snowdon 1982). We assessed the function of the vocal displays using Smith's (1977) approach of observation of individual behavior associated with the displays. Finally, we investigated the function of a complex advertising vocalization of male murrelets, which resembles passerine song in some respects.

In British Columbia, Canada, Ancient Murrelets nest on the conifer-forested slopes of islands within a few hundred meters of the sea. Colonies are visited only during the brief nesting season (April, May, and June). Breeding pairs incubate their clutch of two eggs for about 32 days in 2- to 4-day shifts, then accompany the precocial young to the sea a few days after hatching (Sealy 1976; Jones et al. 1987a, 1987b). On active nights at the colony, large numbers of murrelets perch in trees and on stumps and perform a variety of conspicuous vocal displays.

METHODS

Our study was conducted at Reef Island in the Queen Charlotte Islands, British Columbia, Canada (52°52'N 131°31'W) during April, May, and June of 1984 and 1985. A colony of approximately 5,000 pairs of Ancient Murrelets occupied steep slopes along the north and southeast shore of this island. We obtained 25 hr of recordings of murrelet vocalizations involved with activities including flights over the colony, perching in trees, agonistic and other interactions on the nesting slope, communication between parents and offspring, and rafting of groups of adults at sea. We used Uher 4000 Report Monitor, Marantz PMS-220, Sony TC D5M and Sony WM D6M tape recorders and Audiotecnica AT-801 microphones mounted in Dan Gibson parabolic reflectors to make the sound recordings in the colony and at sea. To record murrelets in burrows, we used the Marantz cassette recorder and Realistic miniature microphones (33-1052

and 30-1056) placed in the nest chamber. To establish the situations in which various vocal displays were used at night, we used a Star-Tron Mk 303A night vision scope or a small light to watch murrelets on the nesting slopes and on the sea near the colony.

The structure of murrelet vocalizations was studied using a real time sound spectrum analyzer (Uniscan 4500 FFT) and a Kay 7800 digital Sona-Graph at the wide band setting (150 Hz over the 16 kHz range). The vocal repertoire was compiled by identifying structurally distinct sounds present in vocalizations of each of many individuals. Later, contextual information was used to examine how each of these displays was used. Vocal displays were assigned names describing their form or representing how they sounded to us. We used Smith's (1977) method of classifying the general messages of vocal displays. This involved the inference of message from the performer's characteristics (e.g., age, sex, breeding status) and our qualitative observations of concurrent and subsequent behavior. We assessed inter- and intra-individual variation of the *chirrup*, a common vocalization of Ancient Murrelets, from measurements of sound spectrograms. We analyzed *chirrups* recorded in three situations: (1) adults calling to young, (2) pair members interacting in burrows, and (3) *chirrup* elements of vocal advertising from tree perches (*song*, see below). We sampled 10 calls from each of 10 individuals from *song* and adults calling to young, and seven calls from each of six individuals calling in burrows. Replicates of *chirrup* elements were obtained from consecutive series of vocalizations from unmarked adult birds recorded from different parts of the colony (singers) or at different burrows (pair members at burrows, and adults departing the colony with young).

Nine temporal and frequency characteristics were measured from the peaks of the chevron-shaped tracings of the spectrograms (Fig. 1). A count of the chevron-shaped tracings (number of peaks) was used as a 10th characteristic. Individual variation was quantified with ANOVA and Kruskal-Wallis tests. To test for differences in the *chirrup* vocalization between the sexes, the calls of 25 known pairs (recorded at their nesting burrow) were measured. Because we did not capture the birds, we could not determine the sex of each individual recorded. We assumed that each mated pair consisted of a male and a female. Differences between the calls of mates (based on Euclidean distances calculated from standard-

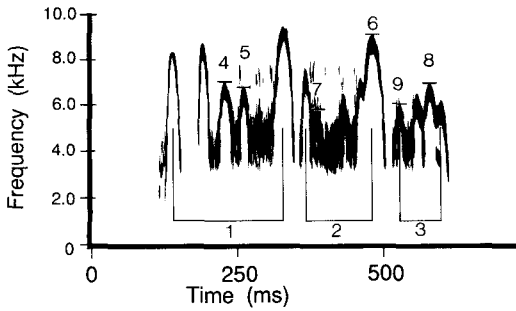


FIGURE 1. A *chirrup* call showing the variables analyzed: (1)–(3) = durations of first, second and third parts (measured peak to peak), and (4)–(9) = frequency maxima and minima of each part (first and last chevrons of first part excluded because of frequent difficulty with measurement due to indistinct peaks), variable 10 was the number of peaks (chevrons) in the entire call.

ized scores of the call characteristics) were compared to differences between randomly selected pairs of calls to examine whether *chirrup* calls were sexually dimorphic, converged within pairs or differ randomly. We used ANOVA to test for differences among the *chirrups* from the three situations, using 25 individual adults' calls to chicks, 23 individuals' *chirrups* from *song*, and 10 individual calls from burrows.

We investigated the function of the vocal advertising display with a simple playback experiment. Playback of recordings of *song* was presented to 10 arbitrarily chosen singers using a cassette recorder and two Aiwa SC-A2 speaker amplifiers. Playback was presented from the forest floor to singers within approximately 20 m of the speakers. The birds' responses were recorded using a Sony WM D6M recorder and a parabola mounted microphone. We also examined the use of variants of *song* in recordings of 22 undisturbed singers. To determine their sex and status, six singers were captured, and later

sexed using a discriminant function based on external measurements (Jones 1985) and another six were collected by shooting and sexed by dissection.

RESULTS

THE VOCAL REPERTOIRE

We identified nine displays in the vocal repertoire of the Ancient Murrelet. Six of the nine vocalizations consisted of sequences of rapidly frequency-modulated elements which appeared as series of chevron-shaped tracings in sound spectrograms. The peak frequencies (4–10 kHz), duration (ca. 10–40 msec), and spacing (20 msec > 1 sec) and continuity of the chevrons were used to distinguish displays of this form. The other three vocalizations included two displays of pure tone (whistle-like) and one with variable atonal (harsh) sounds. The amount of frequency and amplitude modulation and the length of the sounds were used to distinguish the tonal and atonal vocalizations. Most murrelet sounds were easily placed into one of the nine categories, with unclassifiable or ambiguous vocalizations encountered rarely. Most of the vocalizations were used in a variety of situations (Table 1).

CHIRRUP

Chirrups were the most frequent vocalization of the Ancient Murrelet. They were usually uttered as a short call, performed in many situations both by day and night, but were also incorporated within more complex vocalizations such as in *song*, and often occurred contiguously with other displays. For measurement purposes, we divided the *chirrup* into three parts (Figs. 1, 1–3). The parts were readily distinguishable, usually being separated by short silent gaps. Temporal discontinuities occurred throughout the vocalization, but the three parts were identifiable in the *chir-*

TABLE 1. Occurrence of vocal displays in various situations.

Situation	<i>chirrup</i>	<i>chip</i>	<i>song</i>	<i>bubble</i>	<i>trill-rattle</i>	<i>wheeze/ rasp</i>	<i>whistles</i>	<i>chatter</i>
Small groups at sea	***	***	—	—	—	—	—	—
Staging area	***	***	*	***	—	**	*	***
Adults-young (colony)	***	***	—	*	—	—	—	—
Flying over colony	***	***	—	—	—	—	—	—
Singers	*	***	***	—	***	*	—	—
Interaction on forest floor	***	***	***	***	**	*	—	—
Mates in burrow	***	***	*	***	***	***	***	***
Fights	**	**	—	—	***	*	—	—

Frequencies: *** heard whenever this situation was observed, ** usually but not always heard in the situation, * heard at least once in the situation during this study, — never heard in this situation.

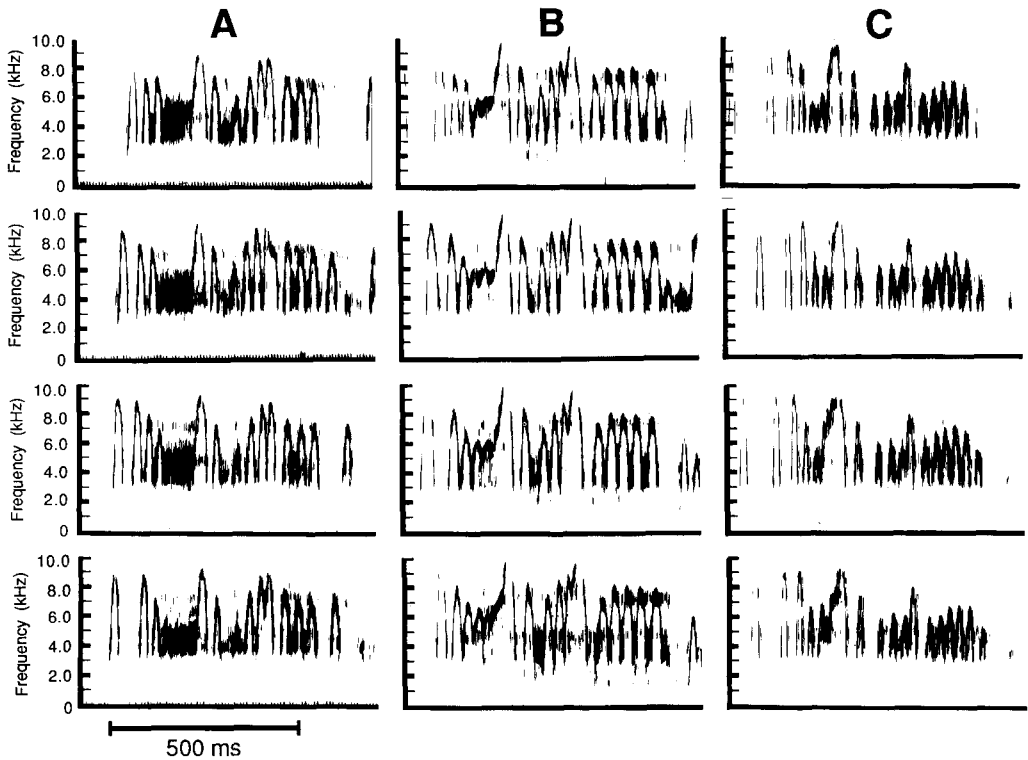


FIGURE 2. Examples of the *chirrup* element of *songs* (complete *songs* illustrated in Figure 5) performed by three different adults at the colony. The four examples in each column belong to individuals A, B, and C.

rups of all murrelets recorded, and served as useful subunits for the measurement of individual variation. Spectrograms of *chirrup* components contained within *song* illustrated the individual stereotypy of this vocalization (Fig. 2). See Jones et al. (1987a) for a similar presentation of the *chirrup* calls performed by adults during colony departure. ANOVA (variables 1–9) and Kruskal-Wallis tests (for variable 10 which was not normally distributed) indicated that all 10 variables of the *chirrup* from three situations exhibited greater variation among individuals than within individuals, consistent with individual stereotypy (Table 2). The sole exception was variable 10 of *chirrup*s from birds in burrows. The stereotypy present in our samples of consecutive calls applies to all *chirrup*s of an individual, as indicated by the identical structure of *chirrup*s recorded at each of 10 burrows on widely separated dates (individuals identified from nesting burrow). Based on the variables measured, the calls of members of 25 presumed pairs were neither more nor less similar than calls of birds chosen randomly (*t*-test comparing mean Euclidean dis-

tance among 25 mated pairs' calls to the mean distance among 50 randomly selected calls, $t = -0.537$, $P = 0.5939$, two-tailed). Thus there is no evidence for either convergence or sexual dimorphism of mates' calls. Three of the 10 *chirrup* variables showed significant differences among the three situations (ANOVA, Kruskal-Wallis $P < 0.05$). The major difference among *chirrup*s from different situations lay in the third part, which had the most elements in *song*, and the least in burrow *chirrup*s. However, individual distinctiveness was maintained across different situations, as indicated by the very similar 'burrow' and 'family departure' *chirrup*s within four individuals for which recordings from each situation were available. The *chirrup* was performed in a wide variety of situations (Table 1), making its 'behavior selection message' (BSM, Smith 1977) very general. The display was associated with a high probability of locomotory behavior (often performed before taking flight) and elevation of the intensity of interactions (performance intensity of agonistic or courtship interactions). Used in interactions of mates, and

TABLE 2. Individual stereotypy of variables of *chirrup*s occurring in three situations, as indicated by ANOVA.

Variable	Departure <i>chirrup</i>		Song <i>chirrup</i>		Burrow <i>chirrup</i>	
	CV	F-value	CV	F-value	CV	F-value
1	7.73	48.7***	7.87	23.1***	9.08	13.0***
2	3.69	230.8***	4.28	114.0***	7.83	35.0***
3	9.30	200.9***	9.67	142.7***	8.35	103.1***
4	5.14	22.2***	5.14	13.9***	5.68	5.1**
5	8.90	16.1***	8.90	19.2***	5.41	15.9***
6	2.85	135.9***	2.85	84.4***	3.88	82.8***
7	7.10	64.6***	7.10	30.3***	8.62	41.2***
8	3.45	61.6***	3.45	49.5***	5.54	7.5***
9	6.05	38.4***	6.05	50.7***	6.23	3.1*
10	4.94	39.7***	4.94	120.5***	5.75	ns

Chirrup variables are as indicated in Figure 1. CV, coefficient of variation. *Chirrup* variable 10 analyzed with Kruskal-Wallis test. * $P < 0.05$, ** $P < 0.005$, *** $P < 0.0005$, ns = not significant. $n = 10$ calls from each of 10 individuals departing with young and singing, and seven calls from each of six individuals in burrows.

parents with young, the *chirrup* also may signal receptiveness to interaction or likelihood to provide parental care.

CHIP, BUBBLE-CALL, CHATTER, AND TRILL-RATTLE DISPLAYS

These four displays consisted of elements similar to those of the *chirrup*, but were less complex and lacked individual stereotypy. The displays differed in the temporal spacing of their elements: *chips* consisted of single chevron elements (<1 per sec), *bubble-calls* and *chatter* had more rapidly used elements (ca. 15 per sec), and *trill-rattles* even more rapid elements (>30 per sec). Little intergradation of these displays occurred, making them readily identifiable from recordings.

The *chip* was the simplest vocal display of Ancient Murrelets. It appeared as a single chevron-shaped tracing, or as two closely spaced vertical traces, in sound spectrograms (e.g., Fig. 3A), peaking above 8 kHz and of 15–25 msec duration. Sounds similar to the *chip* occurred as elements of the more complex displays. *Chip* displays were distinguished by being temporally separated (>500 msec) from other sounds. This vocalization commonly preceded other vocal displays, particularly *chirrup* calls, but was often performed singly by birds in flight or about to take flight, either from the sea or colony, suggesting that it carries a locomotory message.

The *bubble-call* (Figs. 3A, B) consisted of a bubbling-sounding series of chip-like notes, often used by a bird interacting within a meter of another. *Bubble-calls* were identified in sound spectrograms by the presence of widely (50–150 msec) and irregularly spaced chevrons of vari-

able structure, most often occurring in a series lasting a few seconds (e.g., Fig. 3A) producing a stereotyped sound unlike any other vocal display. *Bubble-calling* was frequently given by birds interacting with or in close proximity to individuals performing song (see below). This often occurred high (10–35 m) in trees and also during interactions of pairs near burrow entrances. In interactions involving two birds, *song* and *chirrup* calls of one bird were typically followed by *bubble-calls* and *chirrups* of the other, often occurring as a continuous vocalization. Birds performing *song* were never heard using the *bubble-call*. *Bubble-calling* was also frequently performed during interactions of presumed mated pairs within burrows and by birds interacting at their offshore staging area.

Trill-rattle calls were brief (300–500 msec), rapidly frequency- and amplitude-modulated vocalizations with a distinctive rattling sound. In spectrograms, these appeared as short, rapid series of similar, regularly spaced, chevron-shaped elements (e.g., Figs. 3C–F). *Trill-rattles* were performed by birds in an agitated or aggressive state, usually during interactions of closely spaced birds. *Trill-rattles* were used by birds fighting (pecking and grasping with bills and beating with spread wings) and often occurred just prior to attacks (Fig. 3F1, F2). The call was often the first heard after the entry of an occupied burrow by another murrelet, preceding the complex simultaneous calls of mated pairs (since we could not see inside burrows, we could not determine whether the incubating or arriving bird gave the call). Furthermore, the *trill-rattle* was often incorporated into *song* (see below) and other bouts of complex vocalization. *Trill-rattles* appear to convey an

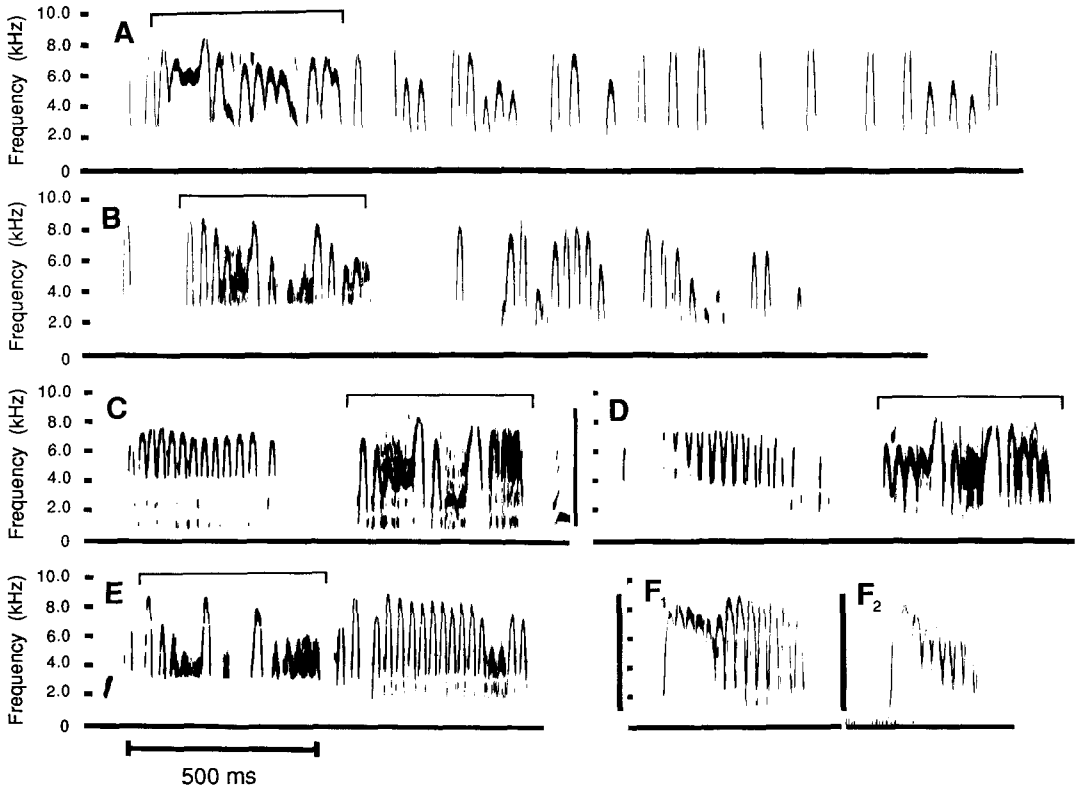


FIGURE 3. Examples of *bubble* and *trill-rattle* calls. A. *bubble-call* from a departure of a family group (note widely spaced *chip* elements). B. *bubble-call* from an interaction in tree. C, D. *trill-rattles* from burrows. E. *trill-rattle* from an adult departing with chicks. F1, F2. *trill-rattles* from a fight. *Chirrup* calls are indicated by horizontal brackets.

agonistic BSM, signalling a high probability of attack.

The largest variety of vocalizations was performed by birds in burrows (Table 1). Loud, rapid vocalizations occurred when off-duty birds returned to the burrow where their mates were incubating (Figs. 4A, B). *Chattering*, the use of rapid bursts of contiguous variable chevron elements (Figs. 4A, B), was the most frequently performed vocal display of murrelets in burrows. *Chattering* may signal a high state of arousal and receptiveness in courtship situations.

PURE TONE AND WIDE-BAND VOCALIZATIONS

Two whistle-like vocal displays were uttered. One consisted of unmodulated notes up to 3 sec in duration (*long whistles*, Fig. 4C, often preceded by a *chip*) and the other consisted of series of short, somewhat frequency-modulated notes (*short whistles*, each of ca. 200 msec duration,

ca. 3 per sec, series lasting up to 5 sec; e.g., Fig. 4D). These calls were used almost exclusively by presumed mated pairs in burrows. One atonal vocal display was used, an unstructured *wheeze* (Figs. 4E–G) which was highly variable and graded into a harsh screech (Fig. 4G). Like the ‘*whistle*’ displays these vocalizations were rarely used except by pairs in burrows, usually following the *chirrup*s and *chattering* that accompanied the entry of burrows by off-duty members of pairs. Harsh *wheeze* calls were performed by murrelets fighting, and by birds being handled by us during banding. These displays are associated with a high level of interaction, but we were unable to assess their BSMs because it was not possible to observe pairs in burrows.

SONG

Song was a frequently heard vocalization, consisting of *chirrup* components incorporated into distinctive rhythmic series of *chip*-like notes (Fig.

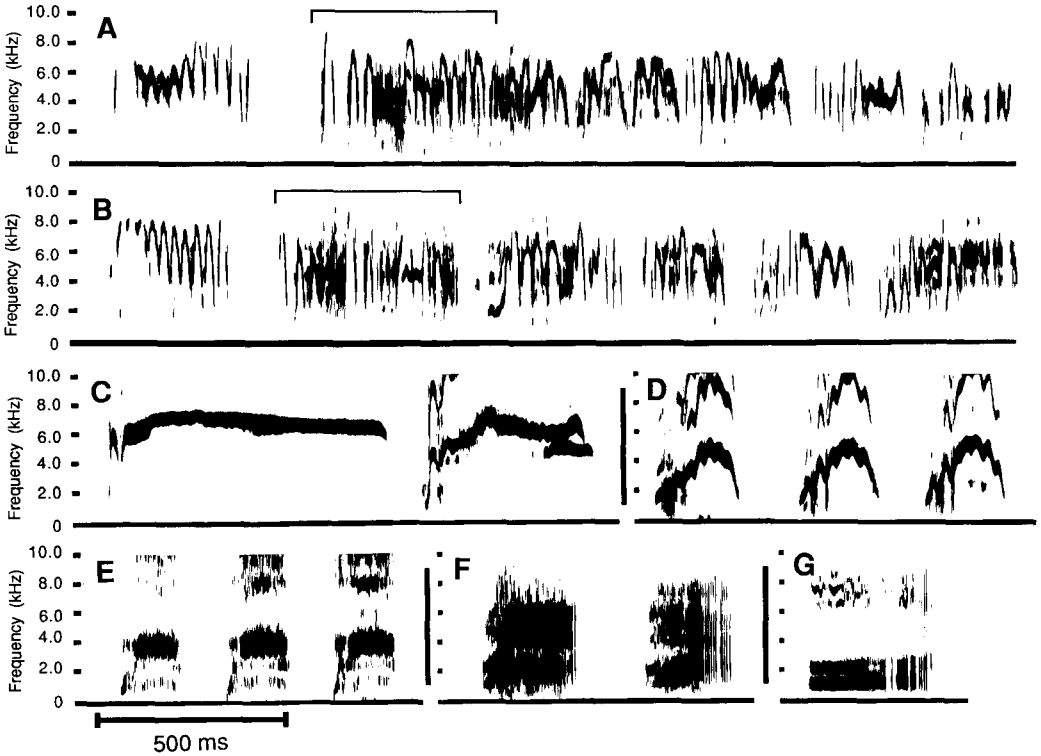


FIGURE 4. A, B. Examples of *chatter* displays following the entry of burrows. A. With overlapping *chirrup*s of each member of pair. B. With one *chirrup*. C. *Long whistles*. D. *Short whistles*. E, F, G. Examples of atonal (harsh sounding) displays, all from interactions of mated pairs in burrows. *Chirrup*s are indicated by horizontal brackets.

5). We used the term *song* to refer to this display because of the circumstances in which it was performed and because it was apparently used only by males (see below). We recorded *songs* with one, two, three, uncommonly four, and rarely five or six *chirrup*s within the rhythmic series; two-*chirrup* *songs* were the most frequent. The presence of the *chirrup* element within *songs* was apparent to us only after careful examination of sound spectrograms. Singing rates were quite variable, but *songs* were most frequently performed at 20- to 30-sec intervals (Fig. 6). *Song* was most often performed by murrelets perched in trees and occasionally by birds on the ground, in burrows, and at the offshore staging area. Murrelets performing *song* ('singers') from tree perches were usually high above the forest floor (10–35 m) and often not visible even when searched for with a bright flashlight. Singers were present at the colony throughout April, May, and June, but their numbers were highly variable from night to night (Jones 1985). Several individuals

had *songs* sufficiently distinctive to be identifiable by ear and were heard from the same location on successive nights. One bird heard on 10 nights in 1984 returned and was recorded at the same location in 1985. Another bird was heard singing from a tree-top location on a different study plot on 25 nights in April, May, and June of 1985. Although we could not determine the proportion of singers that performed from the same location on different nights precisely, it was clear that many did return. The identities of these birds were confirmed from sound spectrograms of the individually distinctive *chirrup* component of their *songs*. The numbers of singers present over a part of the colony was always far fewer than the number of nesting burrows in the same area. Singers were observed and heard engaging in apparent courtship with nonsinging birds (e.g., by one member of mated pairs in burrows), and in agonistic interaction with near-by singers.

Murrelets frequently performed *songs* in re-

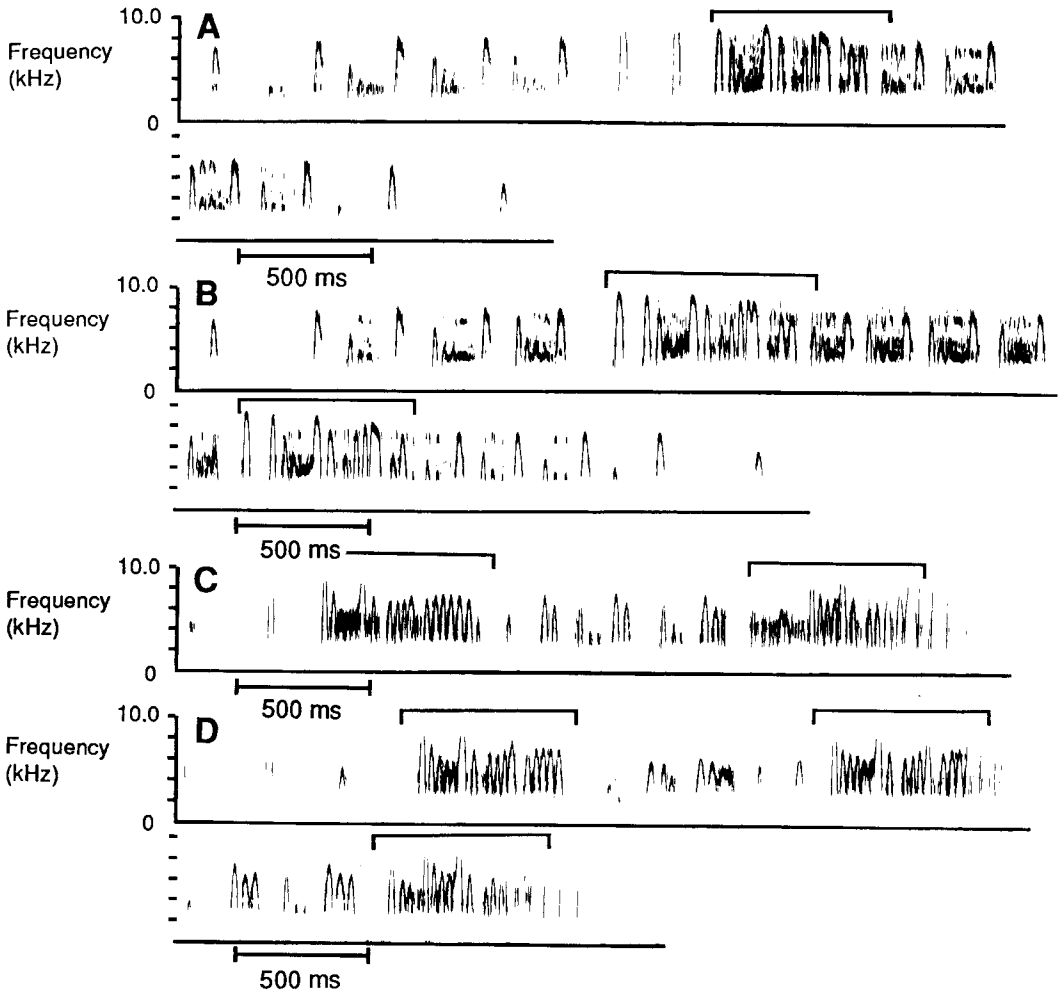


FIGURE 5. Examples of various forms of song. A. with a single *chirrup* (indicated by bracket) and preceding and following *chip* series, 7 May 1984. B. same bird as A, two-*chirrup* song. C. two-*chirrup* song with abrupt beginning and ending, 29 April 1984. D. same bird as C, three-*chirrup* song.

sponse to the *songs* of other individuals. We infer this from the observation that in natural series of *songs* by two singers, one bird's *songs* often followed another's within seconds. This interactive singing or countersinging was recorded for up to 45 min from groups of two or more singers. Murrelets frequently paused in mid *song*, allowed another bird to finish its *song*, then resumed. *Songs* in response to one-, two-, and three-*chirrup* *songs* (performed within 3 sec of another's *song*) did not differ significantly from spontaneous *songs* in the number of *chirrups* performed (χ^2 , $P > 0.1$), suggesting that there was no tendency for matching of *song* form by countersingers. The intervals between successive one-,

two-, and three-*chirrup* *songs* differed significantly ($\bar{x}_1 = 36.1$ sec, $\bar{x}_2 = 42.3$ sec and $\bar{x}_3 = 69.9$ sec, $n = 465$ *songs*, Kruskal-Wallis, $P < 0.05$), indicating that murrelets paused longer after more complex performances. A conspicuous form of *song* variation involved the addition of *trill-rattles* within the *song*, immediately following the *chirrup* component (e.g., Fig. 3E, Figs. 5C, D). *Trill-rattles* followed the final *chirrup* of some *songs* and followed each of several *chirrups* of others, but rarely followed the first *chirrup* of *songs* or were included in single *chirrup* *songs*. Most important, *trill-rattles* were much more likely to occur in responding *songs* (59%) than spontaneous *songs* (33%) (χ^2 , $P < 0.005$) and

were frequently used in countersinging duels, further emphasizing their agonistic function.

The response of singers to playback *songs* was highly variable. Two birds performed *songs* seemingly randomly with respect to the playback *songs*. However, four other singers performed their *songs* directly following each playback *song* or simultaneously with the playback. The remaining singers stopped vocalizing after the playback began. Nonsinging birds landed near the playback speaker during each *song* presentation and approached the speaker, as if searching for the singer. We were unable to capture these birds and ascertain their sex. Although the simple playback trials yielded insufficient data for detailed analysis, the results provided further evidence that singing murrelets responded to other's *songs* and that *song* attracted other murrelets.

Of six murrelets captured and sexed using a discriminant function based on external measurements (Jones 1985), five were males and one was not identifiable. Each of six singers collected and sexed by dissection was male. These results suggested that all singing Ancient Murrelets may have been males. All but one of the 12 singers were nonbreeders, as indicated by the absence of brood patches, suggesting that late in the nesting season (at the stage when breeding birds were departing with chicks, when the birds were captured and collected) most singers were nonbreeding birds. However, the conspicuous singers of the prelaying and laying periods earlier in the season were probably breeders, since few nonbreeders were present at the colony at that time (Gaston, unpubl. data). *Song* appeared to convey a variety of BSMs, including the seeking of and receptiveness to interactions (directed to females, at least when performed in burrows), and as a threatening signal to other males.

DISCUSSION

ORGANIZATION OF VOCAL REPERTOIRE

Ancient Murrelet vocalizations showed a hierarchical form of organization, in that the more complex displays were composites of simpler vocal elements which may be performed on their own. For example, the *chip*, a very short rapidly frequency-modulated vocalization, was often performed alone as a separate display. However, elements identical or similar to *chips* were also performed in rapid, nearly continuous sequences to form distinct vocal displays such as the *chir-*

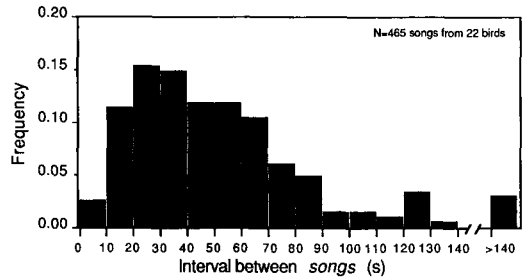


FIGURE 6. Frequency distribution of intervals between *songs*.

rup, *trill-rattle*, and *bubble-call* displays. At a higher level of organization, these composite displays were themselves combined to form longer and more complex vocalizations. For example, *chirrup*s and *trill-rattles* occurred as contiguous components of *song*, and *chirrup-bubble* and *chirrup-trill-rattle* composites were used in other situations. This hierarchical form of repertoire organization is similar to that described for other birds such as Eastern Kingbirds (*Tyrannus tyrannus*, Smith 1966) and Pigeon Guillemots (*Cephus columba*, Nelson 1985). Ancient Murrelet vocalizations have simple combinatorial properties in that they consist of a few acoustic elements combined in various sequences to produce a variety of vocal displays with different functions (see Hailman and Ficken 1986).

REPERTOIRE SIZE

We categorized Ancient Murrelet vocalizations into nine different displays (*chip*, *bubble-call*, *trill-rattle*, *chatter*, *chirrup*, *song*, *long-whistle*, *short-whistle*, and *wheeze*), based on structure. Although we occasionally encountered vocalizations intermediate between some displays, these were very infrequent, suggesting that our classification partitions the repertoire into approximately natural categories. Unfortunately, vocal repertoires have been studied in detail in only two other alcid species: Common Murres (*Uria aalge*, Tschantz 1968) have about 10 vocal displays and Pigeon Guillemots (Nelson 1985) have nine. The Dovekie (*Alle alle*) has at least six vocal displays, based on a less detailed study (Ferdinand 1969, Cramp 1985). The Ancient Murrelet repertoire is similar in size to those described for some other diurnal alcids studied, so there is little evidence that their repertoire size is specialized for nocturnal use. Furthermore, murrelets have a repertoire similar in size to passerines such as

Black-capped Chickadees (Ficken et al. 1978), Purple Martins (*Progne subis*, Brown 1984), and White-crowned Sparrows (*Zonotrichia leucophrys*, Hill and Lein 1985). Estimates of repertoire size of different species must be interpreted with caution because they may depend on the detail of the study or the preconceptions of investigators. However, the similar size of the Ancient Murrelet repertoire to other bird species is consistent with Smith's (1977) suggestion that vocal repertoires should be limited to a fairly small number of displays, each used in a variety of situations. Nonetheless, the Ancient Murrelet vocal repertoire is larger than that of some Procellariiformes. Studies of the vocal behavior of several nocturnal Procellariiformes have described them as having smaller numbers (one to three) of displays (e.g., James and Robertson 1985). The difference in repertoire size between Ancient Murrelets and the petrels may relate to phylogenetic differences between Charadriiformes and Procellariiformes in the development of vocal apparatus and behavior.

VOCALIZATION STRUCTURE

Most Ancient Murrelet vocalizations have a wide frequency range and rapid amplitude and frequency modulation, characteristics that serve to maximize the locatability of sound to the listener (Konishi 1977, Wiley and Richards 1982). This property may relate to the use of the vocalizations by adults calling to mates or their young on the nesting slope and on the sea in darkness (Jones et al. 1987a, 1987b), when vision would be of little use for locating the caller. Furthermore, the rapid amplitude modulation in the structure of the vocalizations (e.g., the *chirrup*) provides the basis for individually distinctive signature traits, as is found in penguins (Jouventin 1982). Ancient Murrelet parents and offspring separate when they depart from the colony and later reunite on the sea in darkness using recognition of their individually distinctive calls (Jones et al. 1987a). Ancient Murrelet vocalizations consist of complex patterns of *chips* and other rapidly frequency-modulated elements that show greater and more rapid amplitude modulation than some diurnal alcids (e.g., Atlantic Puffin *Fratercula arctica*, see Cramp 1985; Common Murre, Tschantz 1968). Although we have not directly tested it here, Ancient Murrelet vocalizations may show unusually locatable and individually distinctive characteristics, suggest-

ing that their vocalization structure may represent an adaptation to their nocturnal lifestyle. However, the choppy, broad-band structure of murrelet sounds has a possible cost, since dense forest habitat such as that of murrelet colonies rapidly attenuates high frequency sounds and degrades amplitude-modulated signals by reverberation (Wiley and Richards 1982; pers. observ.). Thus *chirrup* calls or other vocalizations given in the colony would not be useful for long-distance communication of information coded in their fine structure, such as individually recognizable properties, although their degradation could provide ranging clues to receivers. Above the colony and on the open sea, where attenuation would be less significant, the *chirrup* call or other vocalizations would likely be effective for communication over longer distances. The *chirrup* call resembles the nocturnal calls of several species of storm-petrel, in that it is performed conspicuously by birds flying over the colony.

James and Robertson (1985) have pointed out that species of nocturnal Procellariiformes with flight calls showed dimorphism of calls (five species), while species without flight calls showed no such dimorphism (six species). Ancient Murrelets possess an apparently sexually monomorphic call that is performed in flight over the colony, but have other calls that may differ between the sexes (e.g., *song*, *bubble*). James and Robertson (1985) suggested that sexual dimorphism in voice may have evolved to facilitate pair formation in species that have aerial calling and presumably other sexual behavior away from the burrow. Ancient Murrelets may fit into this pattern of sex-specific calls in species with flight calls and vocal advertising displays that are performed over the colony. Investigation of the vocal repertoires of other nocturnal alcids would indicate whether the pattern is widespread in both nocturnal Procellariiformes and alcids.

ANCIENT MURRELET SONG?

Ancient Murrelets have a complex vocalization that we refer to as *song*. In general, avian vocalizations have been classified either as *songs* or calls, although this has not been a very precise division. We suggest that *song* is an appropriate term for this vocalization because its use is similar to that of passerine *song*: it is the longest and most complex vocalization of the Ancient Murrelet, is performed by males during the breeding season and is involved with courtship.

Murrelet *songs* are normally performed by birds perching in trees, which is certainly reminiscent of passerine singing behavior, and unusual among the Alcidae. Murrelet *song* appears to approximately fit Smith's (1977) broad definition of *song*: "continuous and regular bouts of vocalization." It may also fit Nottebohm's (1972) more narrow definition: "loud and sustained vocalizations delivered seasonally by males in possession of a breeding or courtship territory," although we observed singing murrelets on only temporary courtship or advertising sites. Although *song* is considered to have a role in territory maintenance in many birds (Falls 1978), we found little evidence for this as a function in Ancient Murrelets. Our evidence did suggest that *song* is a site-specific vocalization at least partly addressed to other males, with *song* variants expressing an agonistic message to competing singers. However, the number of singing birds in an area of the colony was always far fewer than the number of active burrows present, and singing occurred intermittently through the nesting season and was normally performed high in trees, away from the nest sites on the forest floor. Few singers regularly returned to the same location on successive nights, indicating that singing was not associated with lasting 'territories.' The most widely proposed alternative function of *song*, for mate attraction and courtship, seems to be the more likely function of the vocalization, since it was so closely linked to courtship behavior. Courtship of pairs within burrows involved *song*, but interactions in trees between singers and nonsingers giving the *bubble* display appeared to also represent courtship, although we were unable to test this directly. *Song* clearly attracted other murrelets, but we were unable to demonstrate the direct attraction of females by playback of male *songs*. Variation in successive Ancient Murrelet *songs* (e.g., presence or absence of *trill-rattle* element) was related to the context of the display, a signalling system possessed by some passerines (e.g., Yellow-throated Vireo *Vireo flavifrons*, Smith et al. 1978 and Chestnut-sided Warbler *Dendroica pensylvanica*, Lein 1978) and by Pigeon Guillemots (Nelson 1985). It appears that few other alcids have male-restricted advertising vocalizations. For example, male Atlantic Puffins, Common Murres, and Razorbills clearly do not have a vocal advertising display (Cramp 1985), although Pigeon Guillemots (Nelson 1985) and Least (*Aethia pusilla*) and Crested auklets (*A.*

crisatella) do (Jones, unpubl. data), although these are not nearly as complex as Ancient Murrelet *song*. A complex *song*-like advertising signal appears to be useful for mate attraction in Ancient Murrelets because of the nocturnal timing of colony activity and the relatively dispersed nest sites compared to other colonial alcids. Further study may identify ecological or phylogenetic patterns in the evolution of *song*-like male advertising in the Alcidae.

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