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HISTORICAL DIVERSITY OF CORMORANTS AND SHAGS FROM AMCHITKA ISLAND, ALASKA¹

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Abstract. We studied the historical biodiversity of cormorants and shags in the central Aleutians by examining the presence and abundance of bones deposited in two large Aleut middens located on Amchitka Island, Alaska. The temporal range of discrete strata in these deposits was from Russian-era contact to about 2,650 years before present. We found six species in these middens: Pelagic, Red-faced, and Kenyon's Shags (*Stictocarbo* [*Phalacrocorax*] *pelagicus*, *S. urile*, *S. kenyonii*), Double-crested (*Hypoleucus* [*Phalacrocorax*] *auritus*), Japanese (*Phalacrocorax capillatus*) and Pallas's Cormorants (*Compsohalieu* [*Phalacrocorax*] *perspicillatus*), ranked in order of abundance. Historical patterns of abundance differed among species. Japanese and Pallas's Cormorants were most likely chance arrivals to the island; Double-crested Cormorants were not found post-contact and we hypothesize that Arctic Foxes may have extirpated them here; Pelagic and Red-faced Shags have remained in constant proportion over the years and abundances may relate to environmental or climatic change. Little is known about *S. kenyonii*. These results suggest that the diversity of the marine coastal avifauna has experienced dynamic change during the late Holocene and that the distributions of shags and cormorants in particular were different than now known.

Key words: *Phalacrocoracidae*; cormorants; shags; Holocene; biodiversity; Aleutian Islands; midden site; zooarcheology.

INTRODUCTION

Temporal changes in biodiversity may be elucidated by scrutiny of the processes likely to promote change and by analysis of historical patterns of abundance and distribution. Situated in the narrow zone between land and sea, coastal breeding birds can be affected by forces associated with both habitats. Cormorants and shags (*Phalacrocoracidae*) are ubiquitous members of the coastal avifauna; the most common species, Red-faced and Pelagic Shags, are found at most seabird colonies throughout Alaska (Sowls et al. 1978). Their breeding habitat is restricted to cliff faces and their foraging range is limited to near-shore waters (Siegel-Causey 1988). Shags (and cormorants to a lesser extent), therefore, are the

neritic component of a seabird community that also includes more oceanic seabirds such as murre and kittiwakes and thus have potential to indicate dynamic change of the neritic and littoral environments.

Excluding species confined to continental and freshwater habitats, there are seven common species of shags and cormorants in north temperate coastal regions (Siegel-Causey and Litvinenko 1992). Japanese and Great Cormorants (*Phalacrocorax capillatus* and *P. carbo*) are found primarily in Asia, but only the Japanese Cormorant is exclusively marine. Double-crested, Olivaceous, and Brandt's Cormorants (*Hypoleucus* [*Phalacrocorax*] *auritus*, *H. brasiliensis*, and *Compsohalieu* [*Phalacrocorax*] *penicillatus*) are confined to the New World. Olivaceous Cormorants are found throughout South and Meso America, but Pacific coastal populations do not breed much further north than the Tropic of Can-

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cer. Pacific coastal populations of Double-crested Cormorants extend from the Mexican border north to Bristol Bay, Alaska, and have their greatest abundances in the central part of the range. Brandt's Cormorants have the most circumscribed distribution of the three and are most abundant along the Central California coast. Red-faced and Pelagic Shags (*Stictocarbo* [*Phalacrocorax*] *pelagicus* and *S. urile*) bridge the gap between the species discussed above and breed throughout the northern North Pacific basin and Beringia (see Siegel-Causey 1991). In addition, two other little-known species occur in this region. Pallas's Cormorant (*Compsohalieu perspicillatus*), now extinct, was known to breed on the Kommandarskii Islands (Stejneger 1884), which are the far western extension of the Aleutian Islands. Finally, Kenyon's Shag (*S. kenyonii*), closely related to Pelagic and Red-faced Shags, has recently been discovered on Amchitka Island (Siegel-Causey 1991), which is centrally located in the Aleutian Island arc.

At present, only two members of the family (Red-faced and Pelagic Shags) breed in the Aleutian Islands and they represent the most abundant phalacrocoracids in the North Pacific, including the Bering, Chukchi, Japan, and Okhotsk seas. Double-crested Cormorants are known to breed on the Alaska peninsula and nearby localities (esp. Lake Iliamna, Shaiak peninsula), but there are few sightings west of Unalaska Island or north of Bristol Bay (Gabrielson and Lincoln 1959, SOWLS et al. 1978, Kessel and Gibson 1978). Anecdotal reports (Kessel and Gibson 1978, Baird and Gould 1983) suggest changing patterns of distribution of these species, but quantification of these is difficult because of inaccuracies in visual reports, conflicting evidence in historical records and recent accounts of nesting patterns, and, not the least, lack of long-term census data throughout the western parts of this region (see also Yesner 1976, Siegel-Causey and Lefevre 1989 for further discussion).

Recent archeological excavation of Aleut middens on Amchitka Island provided us an opportunity to examine the temporal patterns of biodiversity and abundance of North Pacific cormorants and shags. Accurate reconstruction of early animal and plant communities using material exhumed from middens is possible given that there is sufficient knowledge about the ecology of the past occupants (Dinesman 1977, 1986; Savinetskii and Knyazev 1990). The early in-

habitants of the Aleutian Island chain were exclusively maritime hunter-gatherers and coastal breeding seabirds were an important constituent of their diet (Yesner 1976, 1977). Rigorous comparison of past abundances derived from archeological evidence to present day abundances has shown that the early Aleuts hunted seabirds in amounts relative to their biomass (Yesner 1976, 1981), or in other words, they harvested them in the proportions they occurred in the environment. Thus, it is possible to estimate the past diversity and relative abundance of the marine coastal avifauna of Amchitka Island using evidence like bird bones found in Aleut middens.

Insight into the relationship between phalacrocoracid diversity and environmental change is possible for the northern North Pacific and its marginal seas. The paleogeography (and related disciplines) of this region in the Cenozoic is well-studied, particularly that of the late Quaternary (including Holocene) (e.g., Hopkins 1959–1982, Tolmachev 1970). Understanding the population history of these closely related species should help clarify the overall mechanisms affecting the biodiversity of the greater seabird community of the north. This paper discusses the past and present occurrence of cormorants and shags in the Aleutians and the implications of these findings on their population history in the North Pacific.

METHODS

SPECIMENS

Bird bones were collected from two sites on Amchitka Island (Fig. 1) by employees of Archaeological Research, Inc. during summer of 1968 (Desautels et al. 1971), and were later sorted to family by Dr. Stuart Warter (see Acknowledgments). One midden (site 31) was relatively undisturbed and all strata were intact (Emison et al. 1968). The other (site 36) had been used as foundation for a WWII gun emplacement and subsequently was vandalized, so specimens obtained from this site could not be reliably placed in temporal sequence. Details on the archeological methodology used in the excavation of these middens are given in Desautels et al. (1971) and Cook et al. (1972), and various aspects of the physical and biological environment of Amchitka Island are discussed in Guggenheim (1945), Turner (1970), Armstrong (1971), Isakson et al. (1971), McAlister (1971), Mathisen and Peck (1971), and O'Clair and Chew (1971). The avi-

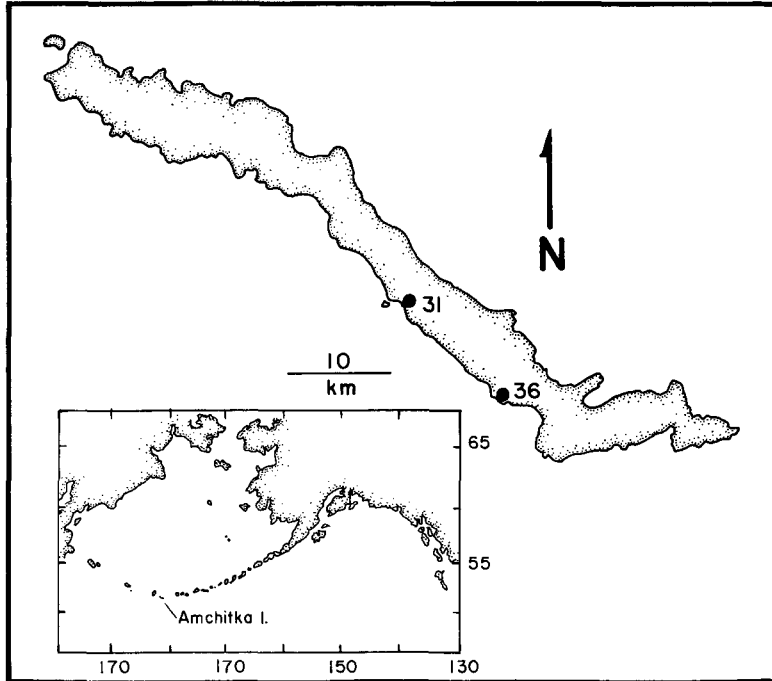


FIGURE 1. Map of Amchitka Island and general area with locations of midden sites.

fauna of Amchitka Island is discussed specifically by Krog (1953), Kenyon (1961), and Emison et al. (1971).

Both midden sites are located on the Pacific Ocean side of Amchitka Island (Fig. 1) and are situated on bluffs 25–30 m above sea level. For the purposes of this analysis, we assume that the collection processes between sites are similar (see Klein and Cruz-Arribe 1984) and thus are directly comparable. The stratigraphy of site 31 was typical of Aleut kitchen middens (see Jochelson 1925, Hrdlicka 1945, McCartney 1971). This midden comprised eleven discrete strata of shell, bone, sea urchin tests, charcoal, and stone artifacts in a sand or humic matrix; detailed analysis is given below. In all, bird bones made up less than 1% of the total weight of the total bones and artifacts removed from both middens (Desautels et al. 1971).

All subfossil skeletal material is kept at CSU Long Beach, and was made available to us through the auspices of Dr. Stuart Warter. Each element was uniquely cataloged and accompanied by data concerning site and stratum. We obtained from various sources (see Acknowledgments) comparative skeletal specimens collected from breeding colonies in Alaska and Beringia; a list

of specimens and museums is available from Siegel-Causey. Voucher specimens of identified elements were deposited with CSU Long Beach.

We calculated the Minimum Number of Individuals (MNI) and Number of Identified Specimens (NISP) indices using the procedures specified by Klein and Cruz-Arribe (1984). For each set of elements obtained from a stratum, we used the largest number of left or right elements as a lower limit to MNI. We derived the upper limit by the sum of the greatest MNI obtained from each level. For NISP, we used the actual number of bones or fragments we identified unambiguously to a species. No other material was considered in this analysis.

OSTEOLOGICAL CHARACTERS

For all elements, discrimination between shags (Leucocarboninae) and cormorants (Phalacrocoracinae) was based on unambiguous qualitative characters that represented the fundamental differences between subfamilies of Phalacrocoracidae (Siegel-Causey 1988). Discrimination among North Pacific shags (i.e., *S. pelagicus*, *S. urile*, *S. kenyoni*) using only qualitative characters was difficult for all elements and, in these cases, length measurements were helpful. There

was little or no overlap in mensural dimensions in this clade (see Siegel-Causey 1991), even between Pelagic and Kenyon's Shags, which are closest in size.

We had little trouble discriminating bones of Double-crested Cormorants from North Pacific Shags. Double-crested Cormorants (and also Japanese and Pallas's Cormorants) are members of a different subfamily (Phalacrocoracinae) than are the shags (Leucocarboninae) (Siegel-Causey 1988). There are diagnostic characters independent of size for nearly every element that make it possible to determine whether a particular bone is from a cormorant or a shag (Siegel-Causey 1988, unpubl. data). For example, shag and cormorant synsacra differ by the number of postacetabular vertebrae (char. 106 of Siegel-Causey 1988) and the pattern of attachment scars of the externus iliofibularis muscle differs among cormorants.

Discrimination among shag bones was effected using characters given in Appendix 1 of Siegel-Causey (1991). Most of the major limb and trunk elements can be identified to species, but in some cases where bones were worn or butchered, they could only be sorted by size. We did not use any such ambiguous shag bones in this analysis. We discriminated among cormorant bones using a large suite of characters (Siegel-Causey 1988, in prep.) and most could be identified by size alone. Double-crested Cormorants are distinctly smaller than Japanese or Pallas's Cormorants. Thus, for the bones of Japanese Cormorants found in the middens, qualitative characters and size were unambiguous. For example, the appearance of the superior surface of the external condyle of the femur is diagnostic for this species (char. 126 of Siegel-Causey 1988). The single carpometacarpus from the Pallas's Cormorant was distinctly diagnostic. The shape of the internal ligamental fossa is triangular and very deeply excavated.

STRATIGRAPHY

Site 31 was the largest midden found on Amchitka Island and measured about 53 m by 29 m. It was located on a bluff about 25 m above sea level and adjacent to a small freshwater stream. The midden lens was 2 m deep in some areas. There were 11 discrete strata in the excavated region of the midden of varying widths and extent: (A) a highly organic humus mixed with sand containing only a few avian bones (This

stratum was not dated, but because it also contained Russian-era artifacts like buttons and trade items, it likely represents post-contact habitation [Desautels et al. 1971].); (B) fine-grained sand, dark clay and charcoal, containing sea urchin tests, limpet shells, and fish, bird and mammal bones—coincident with these were a 30 cm rock fireplace and implements; (C) very fine-grained sand with pebbles containing abundant sea urchin tests with a few limpet shells and bird and mammal bones; (D) fine-grained sand, clay, charcoal with large amounts of fish and bird bones; (E) about 95% sea urchin and limpet shells with scattered fish, bird, and mammal bones; (F) a thin layer of 100% fish bones; (G) fine to medium sand containing some charcoal, sea urchin, limpet and other shells, with fish, mammal, and bird bones; (H) primarily carbon and charcoal with slight amounts of sea urchin tests and sand with fish, bird, and mammal bones—coincident was a 4 m section of a cetacean mandible and a fireplace; (I) fine to coarse sand similar to G but with a higher sea urchin content and much fewer bones; (J) medium-grained sand containing fish, bird, and mammal bones, but no shells; (K) primarily sea urchin tests and sand with a few bird and mammal bones.

Site 36 was located on a steep bluff 30 m above sea level adjacent to a freshwater stream. The midden was approximately 35 by 19 m with a maximum depth of 3 m. Four strata could be distinguished but, because of evidence of subsequent reworking, all strata from this site were combined into a single level and mid-point dating of the predominant subfossil-bearing stratum was used to estimate age of the material.

RADIOCARBON-DATING AND COMPOSITE LEVELS

Radiocarbon dates were obtained from three strata at site 31 (i.e., strata B, G, J) and one at site 36 by the excavators (Desautels et al. 1971). In cases where bone abundances from individual strata were inadequate for quantitative analysis, we combined the data from adjacent undated strata with that from dated strata (i.e., data from strata A and C were combined with data from dated stratum B). We created four composite levels for the data analysis given in Tables 1 and 2: Level I (site 31, strata A+B+C: 890 ± 95 ybp [years before present]), Level II (site 31, strata E+G+H: $1,890 \pm 90$ ybp), Level III (site 36, all strata, $2,250 \pm 100$ ybp), and Level IV (site 31, strata I+J+K: $2,650 \pm 95$ ybp).

TABLE 1. Summary of cormorant and shag bones identified from Amchitka midden sites 31 and 36. Japanese and Pallas's Cormorants were represented by few elements and are not listed in the table.

Level	Date (ybp)	Cranium	Maxilla	Mandible	Sternum	Furcula	Coracoid	Humerus	Ulna	Radius metacarpus	Synsacrum	Femur	Tibio-tarsus	Tarso-metatarsus	Total
Pelagic Shag															
I	890 ± 95	23 (23) ^a	14 (14)	16 (12)	11 (11)	45 (45)	101 (53)	14 (8)	10 (7)	9 (5)	42 (42)	69 (36)	68 (40)	79 (41)	562 (53-371) ^b
II	1,890 ± 90	17 (17)	16 (16)	12 (6)	10 (10)	50 (50)	58 (35)	30 (17)	24 (16)	22 (14)	56 (56)	45 (25)	44 (24)	92 (57)	504 (57-352)
III	2,250 ± 90	6 (6)	5 (5)	2 (1)	5 (5)	14 (14)	43 (24)	17 (10)	6 (5)	7 (4)	6 (6)	45 (25)	29 (20)	36 (21)	251 (25-165)
IV	2,650 ± 95	4 (4)	2 (2)	0	12 (12)	14 (14)	58 (32)	34 (27)	9 (6)	3 (2)	29 (29)	45 (24)	59 (31)	38 (23)	341 (32-225)
Red-faced Shag															
I	890 ± 95	7 (7)	18 (11)	1 (1)	11 (11)	17 (9)	7 (4)	10 (9)	1 (1)	3 (3)	5 (5)	4 (3)	4 (2)	13 (7)	106 (11-78)
II	1,890 ± 90	4 (4)	11 (11)	10 (6)	5 (5)	6 (6)	27 (14)	1 (1)	4 (2)	5 (5)	7 (7)	1 (1)	3 (2)	14 (7)	104 (14-76)
III	2,250 ± 90	4 (4)	2 (2)	6 (4)	1 (1)	4 (4)	10 (5)	1 (1)	2 (1)	6 (6)	1 (1)	0	2 (1)	8 (6)	50 (6-27)
IV	2,650 ± 95	2 (2)	3 (3)	0	0	4 (4)	18 (9)	4 (2)	1 (1)	3 (3)	3 (3)	5 (4)	4 (2)	21 (12)	79 (12-52)
Kenyon's Shag															
I	890 ± 95	0	1 (1)	3 (3)	0	6 (3)	4 (3)	1 (1)	0	—	5 (5)	5 (3)	5 (3)	0	35 (5-24)
II	1,890 ± 90	0	1 (1)	2 (2)	0	3 (2)	1 (1)	4 (2)	0	—	3 (3)	0	0	3 (2)	20 (3-12)
III	2,250 ± 90	0	0	0	0	2 (1)	1 (1)	2 (1)	0	—	2 (2)	2 (1)	0	0	15 (4-10)
IV	2,650 ± 95	1 (1)	0	0	1 (1)	0	6 (6)	3 (3)	0	—	1 (1)	10 (8)	3 (3)	10 (7)	39 (8-34)
Double-crested Cormorant															
I	890 ± 95	0	0	0	0	0	0	2 (1)	0	0	3 (3)	1 (1)	0	0	9 (3-8)
II	1,890 ± 95	0	0	0	0	0	0	1 (1)	0	0	0	0	0	0	3 (2-3)
III	2,250 ± 90	0	0	0	0	0	1 (1)	2 (2)	0	0	1 (1)	0	0	0	4 (2-4)
IV	2,650 ± 95	0	0	0	2 (2)	0	1 (1)	2 (2)	0	0	0	0	1 (1)	0	10 (3-9)

^a NISP (MNI).

^b NISP (MNI; lower limit-upper limit).

TABLE 2. Residual analysis of the distribution (MNI) of element type by strata (Table 1) for the three commonest shags.

Species	Level	Deviation by element type ^{1,2}			
		Skull	Trunk	Upper	Lower
Pelagic Shag	I				
	II		+++	---	++
	III	-	---	-	
	IV	---		+	+
Red-faced Shag	I	+++	++	++	+
	II	+++		-	---
	III	++			---
	IV		--	+	-
Kenyon's Shag	I				
	II				-
	III			+	
	IV		-		++

¹ +, - indicate sign of significant deviation; the number of them, the degree of significance; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

² Skull: cranium, mandible, maxilla; trunk: sternum, furcula, clavicle, coracoid, synsacrum; upper limb: humerus, radius, ulna, carpometacarpus; lower limb: femur, tibiotarsus, tarsometatarsus.

ANALYSIS

We used Correspondence Analysis (CR) to assess the nature of associations between taxa and strata. This multidimensional scaling technique measures the chi-square association between rows (taxa) and columns (strata) of a cross-classified table using correspondence "coordinates" instead of proportions as might be used in a contingency table. A standardized deviate is calculated for each cell of a row or column profile by its relative contribution to the overall chi-square association of the table. Standardized deviates that differ markedly from zero indicate an association (i.e., lack of independence) between a row and column. A cross-product matrix of standardized deviates is computed and is analogous to the covariance matrix of Principal Components Analysis (PCA). This cross-product matrix has r nonzero eigenvalues that sum to the total chi-square association of the table. Thus, the total chi-square information of the comparison table is partitioned into r dimensions. For each dimension (axis), coordinates are computed so that each coordinate axis explains a decreasing amount of the total association. These CR coordinates are analogous to the principal components in PCA that partition the total variance. This feature makes it possible to account for a substantial amount of association between rows and columns by only a few CR coordinates regardless of the number of cells in the table.

Row or column profiles that deviate signifi-

cantly from the average (or marginal) profile will have CR coordinates significantly far from the origin and the chi-square distance is proportional to the deviation. Profiles with similar CR coordinates will have similar associations and thus the chi-square distance between coordinates measures the degree of association between points on a CR plot. The significance of the chi-square distance can be calculated between any two points (Lebart et al. 1984:182), or as done here, a 95% confidence ellipse (CE) can be drawn centered on the origin. Coordinates lying within the 95% CE are statistically equivalent to the mean profile (origin). Greenacre (1984) and Lebart et al. (1984) should be consulted for more detailed discussions of Correspondence Analysis.

Residual Analysis (Haberman 1982, Everitt 1977) makes it possible to isolate sources of deviations from row-column independence in the comparison table. The standardized deviates calculated for use in the Correspondence Analysis can be used to assess the particular nature of association between row and column profiles (i.e., individual cells in the comparison table). In simple terms, the standardized deviate (or residual) is the square root of a chi-square term with the sign of the deviation intact. The residual can be transformed to a standard normal deviate with mean of zero and unit variance with an estimate of term variance calculated from the marginal totals (Everitt 1977, Whittam and Siegel-Causey 1981). The transformation yields an adjusted re-

sidual that indicates the contribution of a cell to the total deviation of the table from independence.

RESULTS

SPECIES COMPOSITION OF MIDDEN ELEMENTS

Of 2,025 bones excavated from the two middens, those of Pelagic Shags predominated (78%). Five other species present, ranked in order of occurrence, were: Red-faced Shag—16%, Kenyon's Shag—5%, Double-crested Cormorant—1%, Japanese Cormorant—two elements, and Pallas's Cormorant—one element. Since all of these midden bones were unarticulated, they represent between 242 and 1,372 (MNI) individual birds (Table 1).

Pelagic Shag. This species was the most numerous and was represented in all strata at both sites (Table 1). Coracoids, tarsometatarsi, femora, and tibiotarsi comprised 60% of the total, with the remaining nine skeletal elements distributed about evenly. Numerical abundance (measured either by MNI or NISP) decreased with age of deposition with half the number found at 2,650 ybp compared to those from Level I of site 31 (890 ybp). In all, these elements represent a range of MNI of between 167 and 1,113 individuals.

Red-faced Shag. This species was second in rank of abundance with 316 skeletal elements (Table 1), representing a range of MNI of between 43 and 224 individuals. Skull bones (cranium, maxilla, mandible) were relatively three times more numerous than was the case with Pelagic Shags and may reflect their greater robustness. Similar to the previous species, abundance decreased with age of deposition to about half the MNI at 2,650 ybp compared to the uppermost layer. The total number of elements represent between 43 and 233 individual birds.

The proportion of Red-faced to Pelagic Shags did not differ through time (Kolmogoroff-Smirnoff two-sample test, $P > 0.05$), whether measured using MNI or NISP, by level or individual strata. In every instance, Pelagic Shag bones were about five times as numerous as Red-faced Shag bones except for stratum G (data not shown) where the numbers were about equal.

Kenyon's Shag. This species (see Siegel-Causey 1991 for discussion concerning the discovery and identification of this species) was the third most

abundant component of the midden avifauna (5% of the total). About half of these bones were associated with the lower limb; the rarest elements were sternum and skull bones. The abundance (measured by MNI and NISP) varied greatly by level and site: this species was most numerous at site 36 and in the upper strata of site 31. The total number of elements (CSULB 14011–14119) represent a MNI of between 20 and 80 individuals.

Double-crested Cormorant. We found only 26 elements of this species (CSULB 14120–14145), most of which were associated with the upper limb. This species was consistently a rare component of the midden fauna, never being more than 2% of the total. It is notable, however, that the MNI remained the same throughout all levels at about 2–3 individuals. In total, these bones represent between 10 and 24 individuals.

Japanese Cormorant. We found only two elements (CSULB 14146, 14147) of this species—a synsacrum and femur—and both were from Site 36. These elements showed no evidence of butchering, but have slight carboniferous markings commonly associated with combustive destruction.

Pallas's Cormorant. We found a single carpometacarpus (CSULB 14148) of this species from site 36. This cormorant is extinct and no associated skeletal elements exist (see Siegel-Causey 1988). Fortunately, one of the bones brought back by Stejneger (1884) from a former breeding colony on Bering Island (Kommandarskii Islands, USSR) was a carpometacarpus (USNM 19071), so direct comparison was possible (see pl. 2 of Stejneger and Lucas 1889).

RELATIVE OCCURRENCE OF MIDDEN ELEMENTS

Inspection of Table 1 reveals that certain bones (e.g., humerus, ulna) were encountered far less often than others (e.g., coracoid, femur). For Red-faced, Pelagic, and Kenyon's Shags together, the large bones of the upper limb (i.e., humerus, ulna, radius) and skull (cranium, maxilla, mandible) were significantly less abundant compared to the other elements (Kolmogoroff-Smirnoff one-sample test, $P \ll 0.001$). To determine whether there was differential occurrence of shag bones by species and by level in the middens, we examined the pattern of deviation from expected values of Table 1 using the adjusted residuals calculated for each cell. The distribution of midden bones

TABLE 3. Pattern of taxon abundance (MNI) in strata excavated from site 31 on Amchitka Island.

Taxon ¹	Strata ^{2,3}						
	A + B ⁴	C	E	G	H	I	J + K
STALB	12	9	4	3	5	6	2
NFUL	2	3	3	1	2	10++	2
SHEAR	8	2-	2-	2	2	12	12+++
CANAD	8-	12	29+++	5	3	2---	6
EIDER	12	9	7	5	4	10	3
HARL	7	5	4	1	4	4	4
LARUS	7	3	5+	3	2	4	4
URIA	9	10	7+	2	4	6	2
AETHIA	42	23	18--	9	9	41++	4-
COMB	60	44	39	11	16	43	14
PELAG	32	25	48+++	5	15	25	6
URILE	11	7	12	3	3	5	1

¹ AETHIA: *Aethia* spp., CANAD: Canada Goose (*Branta canadensis*), EIDER: Common Eider (*Somateira mollissima*), HARL: Harlequin Duck (*H. histrionicus*), LARUS: large gulls (*Larus* spp.), NFUL: Northern Fulmar (*Fulmarus glacialis*), PELAG: Pelagic Shag (*Stictocarbo pelagicus*), SHEAR: Slender-billed Shearwater (*Procellaria tenuirostris*), STALB: Short-tailed Albatross (*Diomedea albatrus*), URIA: *Uria* spp., COMB: all other species listed in Table 1 of Harrington (1984).

² All values except for shags of MNIs taken from Harrington (1984).

³ +, - indicate sign of deviation from independence, number of them indicates significance; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

⁴ MNI values for strata A and B, and J and K were combined in this analysis to increase minimum cell values.

was not homogeneous through time, by species, or by type of element (Table 2). The distribution of Kenyon's Shag bones through time generally conformed to expectation, and only four cells had significant deviations from the overall pattern of abundances. By contrast, bones of Pelagic and Red-faced Shags were found in patterns much different than expected from the overall abundances.

The significant distributions of Pelagic and Red-faced Shag bones were nearly symmetrical by class of element. For Red-faced Shags, cranial elements occurred much more frequently in the upper three levels where the lower limb elements which were significantly underrepresented. Bones of the trunk were more common in the uppermost strata and less common in the lowermost strata; this pattern was directly opposite to that shown by upper limb bones. For Pelagic Shags, the patterns were somewhat less balanced. Fewer than expected cranial bones and more lower limb bones were found in the deepest strata, and a pattern similar to Red-faced Shags of under- and overrepresentation occurred between trunk and upper limb bones in the middle levels.

The patterns of Red-faced and Pelagic Shag bones generally were complementary; for example, an overabundance of Red-faced Shag skull elements in the lowest two layers balanced an underabundance of Pelagic Shag skull elements here. Compared to the overall pattern for shag bones, Red-faced Shags are overrepresented in the uppermost layer while the abundance of Pe-

lagic and Kenyon's Shags conform to expected values.

COMPARISON WITH CONTEMPORANEOUS SPECIMENS

Harrington (1987) surveyed all bird bones from the Amchitkan middens by family and calculated total MNIs for various taxon groups by strata (Table 3). Cormorant bones represented only about 10% of the total number of bird bones excavated from these middens. Table 3 revealed that strata E, I, and J+K differed markedly (E: $G^2 = 41.2$, $df = 11$, $P < 0.001$, I: $G^2 = 30.1$, $df = 11$, $P < 0.001$, J+K: $G^2 = 30.2$, $df = 11$, $P < 0.001$) from the overall pattern of bird bones excavated from site 31. These deviations were caused primarily by the relative numbers of bones from Slender-billed Shearwaters, Canada Geese, small Auklets, and Pelagic Shags. By contrast, Red-faced Shag bones occurred in about average proportions throughout all strata.

Finer discrimination of these patterns was elucidated using Correspondence Analysis. Six CR axes accounted for all of the association between taxon groups and midden strata; however, the first two axes explained 80% of the total association and the model significantly fit the observed abundances ($\chi^2 = 29.5$, $df = 66$, $P = 0.99$). The plot of these two CR axes (Fig. 2) shows several clusters of taxa groups: one comprising shags (PELAG, URILE), one of large gulls (LARUS) and Harlequin Ducks (HARL), three of single taxa each (NFUL, SHEAR, CANAD), and

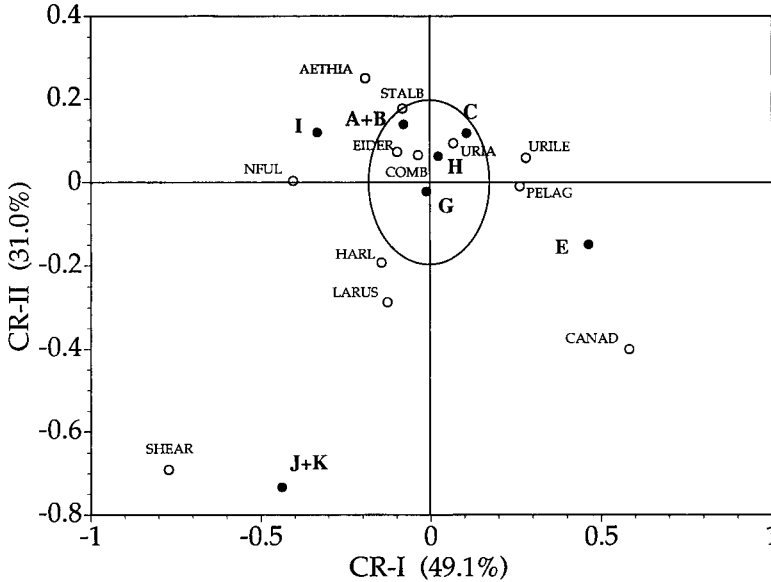


FIGURE 2. Plot of the first two correspondence axes (CR-I, CR-II) describing 80.1% of the total association between midden bones and strata from site 31. The ellipse describes the 95% confidence interval (see text). See Table 2 for explanation of abbreviations.

one large cluster comprising the rest of the species found (see Table 3) in these middens and the majority of the avifaunal diversity here.

The CR plot clearly shows the positive association between the abundances of Canada Geese and Pelagic and Red-faced Shags with stratum E by their proximity of CR coordinates. Pelagic and Red-faced Shags formed a cluster significantly distant ($\chi^2 = 4.55$, $P < 0.01$) from the main cluster of species; that is, their abundance profiles were more similar to each other than to the rest. The Pelagic Shag coordinate (PELAG) lies closer to E than does the Red-faced Shag coordinate (URILE), which reflects its greater association to the average abundance profile there.

Several other patterns are worth noting. First, the abundance profile for Slender-billed Shearwaters (SHEAR) is distinct from the other taxa and is unlike any other in its abundance profile throughout the midden strata. Residual analysis showed that bones of this species were under-represented in relation to the other taxon groups in strata C and E, but was much more numerous than the average in strata J+K (Table 3). The abundance profile of Canada Geese also was distinct; goose bones were more common than expected in stratum E and rare in stratum I. Second, the abundance profiles for Harlequin Ducks (HARL) and large gulls (LARUS) were similar

and distinct from the average profile. Third, the patterns of bone abundances of the remainder of the species identified from the strata excavated from site 31 were overall similar. Since all of these species coordinates fall within the 95% CE, individual profiles in this group cannot be distinguished from one another or from the overall mean profile (origin).

DISCUSSION

Our results indicate that the phalacrocoracidae fauna of Amchitka Island during the late Holocene comprised six species and differed from the present, where only three species are now known to occur (Siegel-Causey 1991). The low level persistence of Double-crested Cormorant bones at Amchitka Island throughout 2,600 years implies a much different distribution of this mesocormorant than presently exists. Clearly, Double-crested Cormorants were more common on Amchitka Island in the past than they are now, but there are several alternative explanations for the patterns observed in these middens. It is possible that a few transient Double-crested Cormorants may always occur throughout the Aleutians due to favorable weather conditions, and these midden bones, therefore, may simply reflect chance occurrences. Another possibility is that since

Double-crested Cormorants appear to prefer warmer climates and waters, subsequent climatic change since 890 ybp (i.e., the most recent mid-den deposits) might have acted to restrict this species from breeding in the central Aleutians in historical times. It is also possible that Double-crested Cormorants always have been a rare component of the Amchitkan avifauna in the past but were extirpated following post-contact introduction of Arctic foxes. Unlike the shags, this species (like all mesocormorants, *Hypoleucis* spp.) prefers level ground for nesting and is an easy target for terrestrial predators (Siegel-Causey 1988).

The Aleutians have been visited by ornithologists for more than a century, and none has observed Double-crested Cormorants further west than Unalaska (Kessel and Gibson 1978). Gabrielson and Lincoln (1959) refer to early accounts of Double-crested Cormorants seen on Agattu Island, west of Amchitka Island; however, these were not based on field-collected specimens but instead on sightings from afar (B. Kressel, pers. comm.). Lack of sightings in recent times could be related to undiscovered colonies or through misidentification, but the former is unlikely given the increased effort in avifaunal censusing of Aleutian colonies (Sowls et al. 1979, Mendenhall and Sowls 1989). Although cormorants and shags fly and feed differently (Siegel-Causey 1988), they are often difficult to identify even at close range (Siegel-Causey 1991) and thus rare occurrences of Double-crested Cormorants in the western Aleutians may have escaped notice from field observers.

A direct link between climate change and shrinking population distributions of Double-crested Cormorants in the Aleutians is problematic. There is fair evidence that the Beringian climate has warmed in the past 800 years (Hopkins 1973, 1979) and if average ambient temperature were the only criterion, this species should be more numerous now on Amchitka Island than in the past. It is clear, however, that other processes have been important. For example, the widespread introduction of Arctic Foxes throughout the Aleutians by Russian traders in the late eighteenth century would have made an effective barrier against widespread dispersal of this flat-nesting cormorant. It is quite likely that Aleutian Canada Geese have suffered a similar fate (Murie 1959, Kenyon 1961).

Our evidence indicates that the other two cor-

morants were probably chance arrivals to Amchitka Island. Japanese Cormorants breed in the Sea of Okhotsk, about 700 km away, and a few transients should be expected during 2,200 years. Friedman (1933) reported finding a humerus of a Great Cormorant in middens excavated on Kodiak Island, 600 km east of Amchitka Island. We have not seen this bone, but it is equally likely that it is instead from a Japanese Cormorant.

Earlier reports (e.g., Pallas 1781, Pennant 1785, Latham 1790, von Kotzebue 1821) of the Great Cormorant in Eastern Siberia, Kamchatka, Kommandarski Islands, etc., should be regarded with caution. Current study in the region indicates that Great Cormorants are primarily continental, and are restricted to isolated populations in the northern Japan Sea (Siegel-Causey and Litvinenko 1992). These individuals were probably Japanese Cormorants, which are similar in appearance. This species ranges north from Japan into the Kuriles and Soviet Far East and post-breeding dispersal or transiency eastward into the Aleutians and Alaska is more probable with this species (cf. Stejneger 1884). Obviously, it will take much more work from this region to settle this question definitively.

The occurrence of a carpometacarpus of Pallas's Cormorant on Amchitka in these middens represents the first evidence of this species from sites other than Bering Island in the Kommandarski Islands. It is possible that this element came to Amchitka by human agency. Cormorant wings (alone or as part of a skin) were never a trade item (Hrdlicka 1945), however, and it does not seem likely that one would have been transported from the Kommandarski Islands by Aleut hunters in kayaks. The existence of flighted, free-ranging Pallas's Cormorants seems a more plausible explanation for this bone on Amchitka Island.

Stejneger (1884) mentions anecdotal reports that place this species on Mednyi Island, Aii Kimur, and other localities in the Kommandarski Islands, but no specimens from these sites are known to exist. There are second-hand reports from early explorers (Pallas 1781, von Kotzebue 1821) that Pallas's Cormorants were used as food by native peoples along the Bering Sea coastlines of Kamchatka. If these reports are accurate, then it is clear that this species had a much larger distribution than was previously estimated. The notion that this species could not fly is unlikely

(see also Stejneger 1884, 1885; Stegmann 1936; Livezey, in press).

The occurrence of Kenyon's Shag on Amchitka Island has been discussed previously (Siegel-Causey 1991). It is not known at present if this species is resident in the Aleutians or if they dispersed eastward from breeding colonies in Kamachatkan or Okhotskian waters (Siegel-Causey and Litvinenko 1992). Little is known about this enigmatic bird.

Our results indicate that Red-faced and Pelagic Shags have been residents of Amchitka Island for at least the past 2,600 years. At present, Pelagic Shags are about five times as numerous as Red-faced Shags on Amchitka (Sowls et al. 1971) and this proportion is generally the same in all of the strata. The strongest pattern of species abundance that we detected among strata was an asymptotic increase in bone abundance with time. This abundance plateau may be partly artifactual, however, because of differential preservation (i.e., bones are preserved better in more recent levels). Also, the integrity of bony elements will depend upon the nature of the soil matrices, i.e., bones are preserved better in calciferous soil (D. R. Yesner, pers. comm.).

The clusters of taxon groups detected by the Correspondence Analysis (Fig. 2) are structured in terms of their abundance by strata, that is, the commonalities of taxa within each cluster relate to the way in which the bones were originally deposited by the early Amchitkans. For example, the cluster comprising Harlequin Ducks and large gulls (HARL, LARUS) are those taxa which were most likely collected inland rather than on the water or on cliffs (Veniaminov 1840, Jochelson 1933). These taxa were exploited apparently for much different reasons: Harlequin Ducks are (were) the most abundant duck of the Aleutian Islands and during breeding season were used as an easy food source. Gulls were eaten only when other food was lacking and collected on land near refuse piles and other human habitations (Jochelson 1933).

The shag cluster may represent a totally different type of functional component. Contemporary reports suggest that shag pelts were a valuable trade commodity and the birds were used as a critical food item primarily in winter (Collins et al. 1945, Hrdlicka 1945). The early Aleuts considered January as *anulgilum tugida*, "the month of uriles [black shags] when they were hunted" (Veniaminov 1840:255). Jochelson

(1933) reported that they were caught by hand in their nests and used for food; winter cormorants were prized at least as much for their neck pelts for capes as they were for the meat.

Early Aleuts used shags for other purposes. The significant underrepresentation of the major bones of the upper limb (Table 1, 2) in these middens results from their use as tools or implements (Jochelson 1933, Desautels et al. 1971). The underrepresentation of skull bones in the middens probably relates to their fragility rather than preferential usage, because it does not appear that these elements had any special use or value (Veniaminov 1840, Jochelson 1933).

These results suggest that the diversity of the marine coastal avifauna has experienced dynamic change since the late Holocene and that the distributions of shags and cormorants in particular were different than now known. Some differences seem likely due to changing environmental conditions in Beringia, but many other factors may have affected species numbers and abundances. Studies underway on material from middens located on nearby islands presage a detailed biogeographic history of coastal seabird populations of the Bering Sea.

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