Holocene record of the Antarctic shag (Notocarbo bransfieldensis) in Fuegian waters

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HOLOCENE RECORDS OF THE ANTARCTIC SHAG (*PHALACROCORAX [NOTOCARBO] BRANSFIELDENSIS*) IN FUEGIAN WATERS[1]

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Abstract. The Antarctic Shag can be discriminated from its congeners by five osteological characters. Using these characters, we were able to identify bones of this species in five shell middens located in southern Fuego-Patagonia. The temporal distribution of these elements extends from historical times (280 YBP) to the middle Holocene (6,100 YBP). These extralimital birds may have reached Fuegian waters through chance events, by postbreeding dispersal, or as vagrants from a yet undiscovered Fuegian colony. We discuss the implication of these and other findings on the specific status of the Antarctic Shag and its sympatry with the Imperial Shag. The current designation of the Antarctic Shag is proposed as *Notocarbo bransfieldensis* (Friedmann 1945).

Key words: Notocarbo; Phalacrocoracidae; blue-eyed shags; Holocene; middens; Fuego-Patagonia; sympatry.

INTRODUCTION

The blue-eyed shags of the Southern Hemisphere are a group of phenotypically similar populations comprising an uncertain number of species and forms. In a phylogenetic study using osteology, Siegel-Causey (1988) was able to discriminate five clades within this group. The current taxonomy recognizes only one genus, *Phalacrocorax,* but his analysis prompted recognition of these clades as genera. One genus, the "western" blue-eyed shags (*Notocarbo* spp.), is confined to the Kerguelen and Crozet archipelagos, Fuego-Patagonia, and Antarctica and the Scotia Arc (e.g., the Kerguelen Shag *N. verrucosus,* the Imperial Shag *N. atriceps* [+ *albiventer*], the South Georgia Shag *N. georgianus,* and the Antarctic Shag *N. bransfieldensis*). Only recently have there been studies on the natural history of this genus (Devillers and Terschuren 1978; Williams and Burger 1979; Shaw 1985a, 1985b, 1986; Siegel-Causey 1986a, 1986b, 1987, 1988), but precise knowledge about the distribution and ecology of these species is lacking.

Least is known about the seasonal distribution of the Antarctic Shag, a common breeding bird of the Antarctic peninsular coasts and Scotia Arc (Watson et al. 1971, Siegel-Causey 1988). The consensus of published studies is that this species stays close to shore during the breeding season and forages near the breeding grounds in offshore waters year-round (Clarke 1906, Murphy 1936, Watson et al. 1971, Bernstein and Maxson 1981). This species has never been collected north of the Antarctic Convergence, particularly in the nearest land to the north, Tierra del Fuego (Humphrey et al. 1970).

Recently, we had the opportunity to examine large collections of subfossil cormorant bones excavated from midden deposits in Argentine Tierra del Fuego and southern Chile. This paper discusses the osteological features and taxonomic status of the Antarctic Shag, its past and present occurrence in Tierra del Fuego, and the implications of its sympatry with the Imperial Shag (*N. atriceps*).

METHODS

Cormorant bones were collected from five sites (Fig. 1) in Argentine Tierra del Fuego and southern Chile by various investigators (Lancha Packewaia and Tunel, Argentina: L. A. Orquera and colleagues; Punta Maria, Argentina: L. A. Borre-

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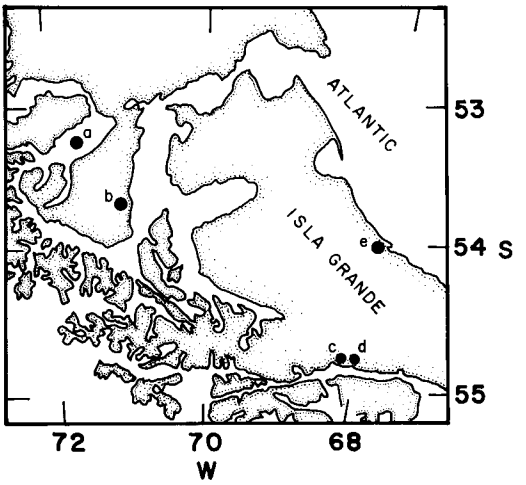

FIGURE 1. Location of midden sites in southern Fuego-Patagonia. (a) Englefield Island, Chile; (b) Bahia Buena, Chile; (c) Lancha Packewaia, Argentina; (d) Tunel, Argentina; (e) Punta Maria, Argentina. Ushuaia is in the vicinity of c and d.

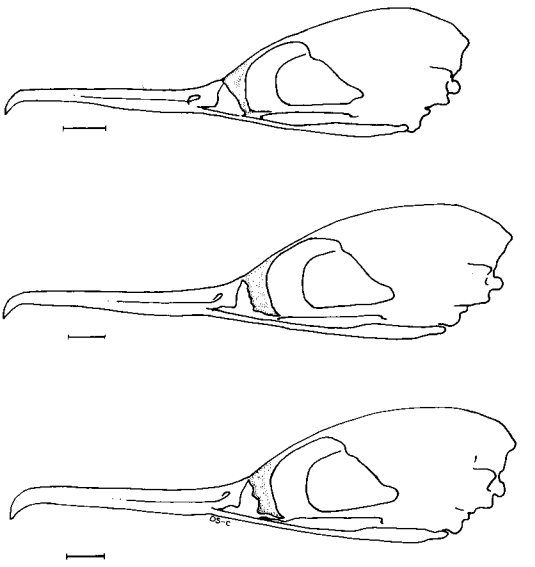

FIGURE 2. Prefrontal (lachrymal) of blue-eyed shags, lateral view (left side). Top: Imperial Shag *Notocarbo atriceps* (KU 78402); middle: Antarctic Shag *N. bransfieldensis* (WSM 38065); bottom; Ushuaia specimen (KU 82210). Line equals 1 cm.

ro; Bahia Buena, Chile: O. Ortiz-Tronsco; Englefield Island, Chile: J. Emperaire). Unlike many other kitchen middens in the region, these five have been relatively undisturbed, and with the exception of the superficial layers, the strata were intact (Orquera, pers. comm; Legoupil 1978, 1980; Piana 1984; Albero et al. 1986).

All subfossil skeletal material is on loan from Asociacion Investigaciones Antropologicas and Instituto de la Patagonia to the Museum of Natural History, Univ. Kansas (KUMNH), and Muséum National d'Histoire Naturelle, Paris (MNHN), and was made available to us through the auspices of P. S. Humphrey, Director of the KUMNH, and D. Legoupil (MNHN). Each skeletal element was uniquely catalogued, and accompanied by data concerning site and stratum. We obtained from various sources (see Acknowledgments) comparative skeletal specimens collected from breeding colonies in Antarctica and South America; a list of specimens and museums is available from Siegel-Causey.

Each of the osteological characters we used was a discrete trait in which at least two discrete states could be defined. We found some characters having modal states in the Antarctic Shag, but in certain cases discrimination between large Imperial Shags and small Antarctic Shags was problematical. We excluded these characters from analysis. Of the four characters used to identify midden remains, least satisfactory was that on the coracoid; where ambiguities existed in interpreting the state of this character, we coded the identity of the bone as unknown.

We calculated the Minimum Number of Individuals index (MNI) using the procedure specified by Poplin (1976). For each set of elements obtained from a station, we used the largest number of left or right elements as an upper limit. We derived the lower limit from the sum of the greatest MNI obtained from each stratum.

Radiocarbon dates have been obtained for most strata in the five middens (Orquera, pers. comm.; Legoupil 1978, 1980; Piana 1984; Albero et al. 1986). Bones from undated strata were not used in this analysis, nor were fragments which lacked the diagnostic characters described below.

RESULTS

Using skeletons of Imperial, Kerguelen, South Georgia, and Antarctic shags collected from breeding sites, we determined that the Antarctic Shag can be distinguished from all other species of *Notocarbo* by five diagnostic osteological characters (Table 1, Figs. 2–6). These characters are found on the skull (shape of the prefrontal), mandible (orientation of the intramuscular line in the subcaudal fossa), coracoid (presence of deep fossa), femur (attachment of M. obturator internus

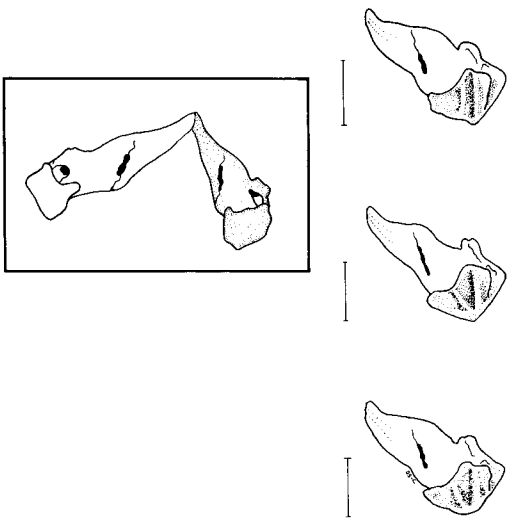

FIGURE 3. Mandible of blue-eyed shags, posterior view of caudal fossa (right side). Inset box shows caudal view of mandible; shading indicates right ramus and caudal fossa. Top: Imperial Shag; middle: Antarctic Shag; bottom; Ushuaia specimen. Specimens listed in Figure 2; line equals 1 cm.

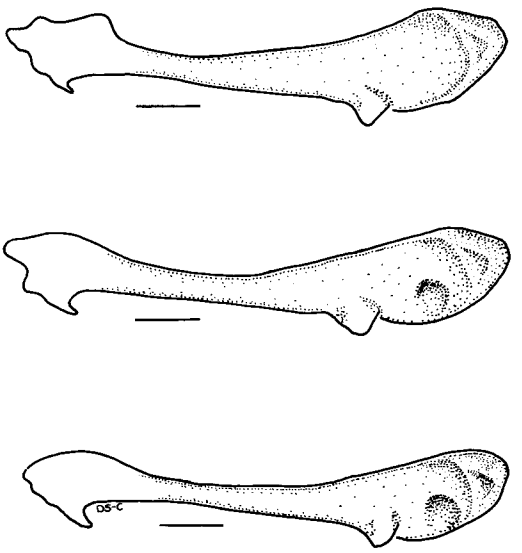

FIGURE 4. Coracoid of blue-eyed shags, medial view (left side). Top: Imperial Shag; middle: Antarctic Shag; bottom: Ushuaia specimen. Specimens listed in Figure 2; line equals 1 cm.

+ externus), and tarsometatarsus (relative size of the internal condyle of trochlea II). Only the latter three of these characters were useful overall for identifying midden bones, since no mandibles and few cranial fragments of cormorants were found in Fuegian middens.

The predominant bird remains found in these middens were those of phalacrocoracids, and of them, the most numerous were bones of the Imperial Shag (Siegel-Causey, Humphrey, and Lefevre, unpubl.). The other species present, ranked in order of their occurrence, were: Rock Shags *Stictocarbo magellanicus,* Olivaceous Cormorants *Hypoleucos brasilianus,* Red-legged Shags *S. gaimardi,* and Antarctic Shags. All but the latter two are common breeding species of southernmost Fuego-Patagonia (Humphrey et al. 1970, Siegel-Causey 1988); diagnostic characters for them are given in Siegel-Causey, Humphrey, and Lefevre (unpubl.).

Of the approximately 3,900 cormorant bones exhumed from midden sites, we identified 78 as from Antarctic Shags (Table 2). Of these, 49 (64%) were tarsometatarsi, 17 (21%) were femora, 10 (13%) were coracoids, and two were cranial fragments, one of which was nearly complete. A list of catalogued specimens, collection sites and strata is available from Siegel-Causey. None of the other elements present in midden deposits (e.g., humerus, tibiotarsus, sternum, digits) showed features which could be used to discriminate between Imperial and Antarctic shags, which are most similar in osteology among those found in the middens. Since the midden bones were unassociated, the MNI these 78 skeletal elements represent ranges between 34 and 53 individuals (Table 2).

Radiocarbon dates indicate a deposition span of about 6,100 years. Because the midden strata at any site did not appear to have been disturbed or reworked, the radiocarbon-dated ages of strata should reflect ages of deposition (i.e., collection by native peoples) for Antarctic Shag bones.

DISCUSSION

TAXONOMIC STATUS

Discrimination of blue-eyed shags is complicated by their overall phenotypic similarity. Previously, the most commonly used criterion was the pattern of the head plumage: all forms with dark feathering extending from the top of the head down to the gape ("dark-cheeked") were classed as *albiventer*; those with dark plumage not reaching the gape ("light-cheeked") were considered *atriceps.* Classification to subspecies was by location, although various phenotypic characters (e.g., caruncle color and shape, face

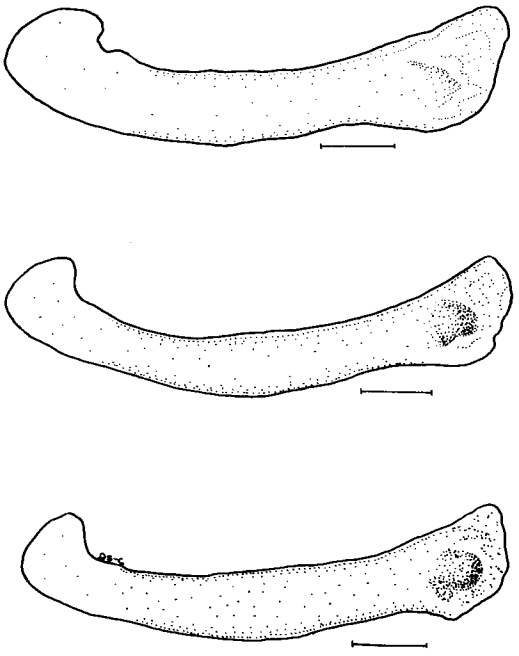

FIGURE 5. Femur of blue-eyed shags, lateral view (right side). Top: Imperial Shag; middle: Antarctic Shag; bottom: Ushuaia specimen. Specimens listed in Figure 2; line equals 1 cm.

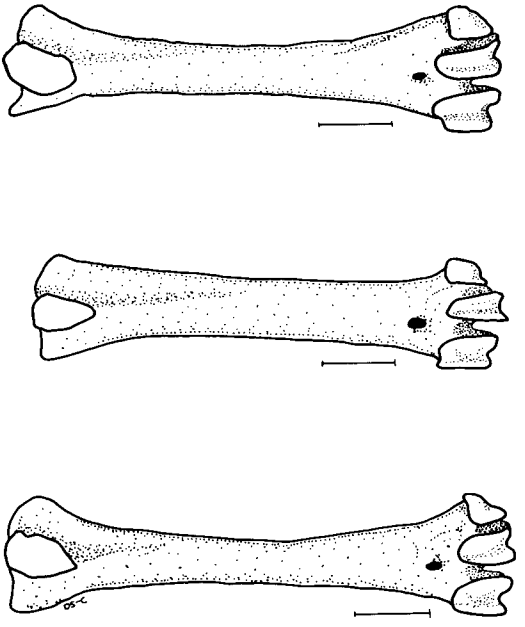

FIGURE 6. Tarsometatarsus of blue-eyed shags, posterior view (left side). Top: Imperial Shag; middle: Antarctic Shag; bottom: Ushuaia specimen. Specimens listed in Figure 2; line equals 1 cm.

color) were used inconsistently and subsequent to identification by other means (see Devillers and Terschuren 1978). Blue-eyed shags of both plumage morphs breed in Fuego-Patagonia, but the predominant morph in Antarctica and the Scotia Arc is light-cheeked. Shags from these latter regions were thus classed as subspecies of the "*atriceps*" form (e.g., *N. atriceps bransfieldensis*).

From the very first studies, however, the taxonomic status of the Antarctic Shag was unclear. Lönnberg (1906) and Bennett (1920, 1926) discriminated between South Georgian Shags and all other blue-eyed shags, but both referred to the Antarctic population as an undefined subspecies. Murphy (1936) examined all forms of the blue-eyed shags present in South American and Antarctic waters (i.e., *P. atriceps* + *albiven-*

TABLE 1. Osteological characters diagnostic for the Antarctic Shag.

Antarctic Shag (*Notocarbo bransfieldensis*)	Congeners (*N. atriceps, N. georgianus, N. verrucosus*)
Cranium: Prefrontal (lachrymal) Fig. 2	
Robust, subquadrate, often with strong anterior projections	slender, superior width at least 1.5× inferior width, anterior edge smooth
Mandible: Intramuscular line in caudal fossa Fig. 3	
Directed medially	directed laterally
Coracoid: Sulcus supracoracoideus Fig. 4	
Deeply excavated, subcircular, well-defined	shallow, margins and shape indistinct
Femur: Attachment of M. obturator externus + internus Fig. 5	
Fossa deeply excised, circular, bounded by rugose projections	fossa shallow, elliptical, margins indistinct
Tarsometatarsus: Internal condyle of trochlea II Fig. 6	
Greatest diameter subequal to that of external condyle	diameter much less than that of external condyle

TABLE 2. Distribution of Antarctic Shag skeletal elements in Fuegian midden deposits.

Age of deposition[1]	Midden site (strata)	Number of elements (MNI)[2]			
		Cranium	Coracoid	Femur	Tarsometarsus
280 ± 85	Lancha Packewaia B[3]		1 (1)	5 (3)	3 (2)
300 ± 100	Punta Maria II				4 (4)
455 ± 85	Lancha Packewaia C[3]				1 (1)
1,590 ± 50	Lancha Packewaia D				1 (1)
4,215 ± 305	Lancha Packewaia E + XY	1 (1)	1 (1)	6 (3)	9 (5)
5,210 ± 110	Bahia Buena I			2 (2)	6 (3)
5,890 ± 120	Tunel	1 (1)	6 (5)	2 (2)	11 (6)
5,895 ± 65	Bahia Buena II				3 (3)
6,070 ± 110	Bahia Buena III			2 (2)	11 (7)
6,100 ± 110	Englefield Island		2 (1)		
Total		2 (2)	10 (8)	17 (12)	49 (31)

[1] Radiocarbon date ± measurement error.
[2] Number of elements is the actual number found; MNI is the Minimum Number of Individuals index calculated from this number (see Methods).
[3] Strata B and C may not be distinct from each other (Orquera, pers. comm.)

ter) and concluded that the prevalence of individuals with intermediate plumage states required additional data for classification. Using mensural characters, he diagnosed the Antarctic population as having longer tails and shorter bills than the rest, but inexplicably did not provide a valid scientific name, designating it only as "*Phalacrocorax atriceps,* subspecies" (Murphy 1936:888). He later (1936:889) stated that ". . . Mr. Bennett has labeled these specimens with a doubtless deserved subspecific name, *bransfieldensis,* which seems, however, never to have been published. In view of the systematic work that remains to be done with the shags from various parts of West Antarctica, I prefer to attempt no further discrimination at present." His contention that "*bransfieldensis*" was previously unpublished is supported in that Bennett (1920, 1926) only referred to Antarctic Shags as "*Phalacrocorax atriceps* subspecies."

Murphy then gave diagnostic characters for various populations in the South Orkney Islands, South Shetland Islands, and the Antarctic Peninsula, and listed a distribution but qualified it as pertaining to "one or more subspecies." A tabular comparison of the mensural features of various subspecies of *P. atriceps* was given earlier (1936:881) in his discussion of the blue-eyed shags.

Friedmann (1945:310) believed that Bennett's unpublished manuscript name was ". . . definitely connected with a description and a locality in Murphy's discussion and is therefore valid from that point in literature," and designated two cotypes (identified as USNM 264141 and 264142 by Deignan [1961:23]). However, because of Murphy's (1936:888) action not to name the Antarctic Shag, and by including various taxa in the description, his subsequent reference to Bennett's manuscript name is excluded as a valid name under Article 1(b)6 of the ICZN. The first valid citation [cf. Article 13(a)1] of a name for this taxon is given by Friedmann (1945:310) at the point where he stated ". . . On the whole, it seems that the Antarctic birds are separable on the basis of the tail length, and they are here considered as *bransfieldensis.*"

McKitrick and Zink (1988) provided objective criteria for assessment of species rank by using a phylogenetic rather than the traditional biological species concept. This requires that species be monophyletic and distinguishable by at least one character. We conclude, therefore, that the Antarctic Shag is a distinct species characterized by five diagnostic osteological features, by the distributional evidence presented here, and by various mensural and behavioral features discussed elsewhere (Murphy 1936, Bernstein and Maxson 1984, Siegel-Causey 1986a). Thus, the original citation of the Antarctic Shag is *Phalacrocorax atriceps bransfieldensis* Friedmann, 1945, and the current designation (cf. Siegel-Causey 1988) is *Notocarbo bransfieldensis* (Friedmann 1945).

DISTRIBUTION IN FUEGIAN WATERS

The presence of Antarctic Shag bones in archaeological sites encompassing six millenia in southern Fuego-Patagonia implies a larger distributional range for this species than previously

TABLE 3. External measurements of Imperial, South Georgia, and Antarctic shags, and an unidentified specimen.

Species	n[1]	Bill length $\bar{x}$ (SD)	Wing chord $\bar{x}$ (SD)	Tarsus length $\bar{x}$ (SD)	Tail length $\bar{x}$ (SD)
South Georgia Shag (*N. georgianus*)	5	46.8 (2.91)	271.2 (8.54)	54.3 (3.67)	121.2 (4.79)
Antarctic Shag (*N. bransfieldensis*)	8	56.6 (3.18)*** t = 3.05[2]	308.7 (14.8)*** t = 3.23	63.8 (3.93) t = 0.56	130.6 (13.21)*** t = 2.83
Imperial Shag (*N. atriceps*)[3]	22	60.2 (2.66)	294.4 (9.41)	62.9 (3.67)	119.9 (7.20)
KU 82210 (collected 28 January 1986, Ushuaia Bay, Tierra del Fuego, Argentina)[4]	1	54	—	66	150

[1] Sexes pooled.
[2] t-values relate to comparisons between Antarctic and Imperial shags.
[3] Specimens restricted to Tierra del Fuego.
[4] Measurements taken from photograph of specimen.
*** $P < 0.001$.

expected. The results presented here are the first to establish the occurrence of this species outside of Antarctica. There are several possible explanations for the presence and temporal distribution of Antarctic Shag bones in Fuegian middens.

These midden bones might represent individuals that moved north from the Antarctic Peninsula up into the Fuegian Archipelago during cold climatic changes in the past. None of our subfossil datings, however, correspond to any cooling period in South America (Markgraf 1980, 1983, 1985; Markgraf and Bradbury 1982). Other alternatives are that the presence of this species in Tierra del Fuego represents only chance events caused or assisted by strong southern storms, that the midden bones are evidence for normal postbreeding dispersal in winter from Antarctica to Fuego-Patagonia, or that there exists a breeding colony of Antarctic Shags in Fuegian waters.

It is possible that all of the Antarctic Shag bones found in the middens were from transient birds. Until more is known, however, about the probability of transiency in Antarctic Shags, and the overall frequency of extralimital birds in Tierra del Fuego (see Humphrey et al. 1970), the likelihood of this hypothesis is unknown.

The postbreeding dispersal conjecture is possible since local Antarctic populations seem to decrease in winter. Antarctic Shags are noted around the breeding areas on the Antarctic Peninsula and Scotia Arc in winter, but in much lesser numbers than in summer (Clarke 1906, Holdgate 1963, Glass 1978, Heimark and Heimark 1984, and others). No site in Antarctica has yet been reported to harbor larger numbers of shags in winter than in summer, thus the fate of the summer birds unaccounted for in winter may be that they overwinter in Tierra del Fuego. There is circumstantial evidence, moreover, that some Antarctic Shags fly northward in fall into the milder Fuegian climates. Ardley (1936) sighted shags on 15 April 1930 at a position 150 miles SSE from Cape Horn heading north and believed them to be Antarctic birds on migration to "the Patagonian Islands." Given the confusing similarity among blue-eyed shags, Ardley's identification of these birds as Antarctic rather than Fuegian species is only suggestive.

The Fuegian colony conjecture is also possible, but its support is enigmatic. In austral summer (28 January 1986), an adult male blue-eyed shag was collected in Ushuaia Bay, Tierra del Fuego, and identified as an Imperial Shag (KU 82210) which are common residents in the Beagle Channel (Humphrey et al. 1970). Later examination of its external morphology (Table 3) and osteology (Figs. 2–6) revealed instead that it was an Antarctic Shag, and distinct from any known specimen of Imperial Shag. The nature of the phenotypic data precludes more robust multivariate comparisons, but the qualitative characters are undeniable. Given the strong external similarity of Imperial and Antarctic shags, the lack of expert observers in this region, the dearth of ringing data, and the minimal exploration of the southern Fuegian Archipelago, the presence of an extralimital breeding colony cannot be discounted. An equally likely explanation is that

this particular bird was a transient from Antarctica.

SYMPATRY WITH THE IMPERIAL SHAG

Six thousand years of Fuegian history would have been ample time for introgression to have occurred between Imperial and Antarctic shags, but this does not appear to be the case. Recognizing Antarctic-Imperial shag hybrids by external features, however, is problematic. The phenotypic similarity of these species precludes reliable identification by plumage or morphology, and usage of typological species definitions as discussed earlier means that both Antarctic and Imperial shags collected in Fuego-Patagonia, and their possible hybrids, will have been identified as the "*atriceps*" form. Mensural characters appear more reliable, but little is known about the extent of individual variation.

In contrast, the osteology is better quantified and thus potentially easier to identify hybrid states. However, we found intermediate states in the osteological characters only on the coracoid, and only in eight (10%) field-identified "Imperial" Shags collected from all Fuego-Patagonia, three of which (KU 78289, 78382, 81206) were collected in the Beagle Channel. Furthermore, the courtship behavior of Imperial and Antarctic shags differs in the performance of certain displays and in the use of unique displays (e.g., Gargling, Hop, Postlanding Kink-throating, Defensive Nest-indicating, Pointing, and Darting) (Siegel-Causey 1986a).

It seems apparent, therefore, that hybrid pairings evidenced by intermediate states or mosaic individuals are rare or even nonexistent for Fuegian populations. In light of these and other data presented here, we consider the Antarctic Shag as a distinct species sympatric with the Imperial Shag, and as a present member of the Fuegian avifauna.

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