The Condor 89:760–766

MOLTS OF THE ROCK SHAG AND NEW INTERPRETATIONS OF THE PLUMAGE SEQUENCE[1]

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Abstract. The Rock Shag (*Phalacrocorax magellanicus*) was found to be similar in molt patterns to other cormorants studied. It was previously thought that two predefinitive plumages occur in this species; this study shows there is only one predefinitive plumage, which is polymorphic and geographically variable. In addition, although the alternate and basic plumages were thought to be very distinct in aspect, I found that these plumages are similar, and specimens previously thought intermediate between alternate and basic plumage combine individual and geographical variation. Differences in frequencies of juvenal plumage phases and adult plumage variants between Chilean and Argentinian coastal populations suggest evolution in isolation by populations separated by a vicariance event such as the Llanquihue Glaciation (20,000 to 10,000 ybp).

Key words: Rock Shag; Phalacrocorax magellanicus; *molts; juvenal plumage; winter plumage; vicariance effects.*

INTRODUCTION

The Rock or Magellanic Shag (*Phalacrocorax magellanicus*) is a small cormorant inhabiting marine coastal regions of southern South America and the Falkland Islands (Fig. 1). No geographic variation has been described in this species, and little has been published on its molts (Murphy 1936). The complex molts of cormorants are not well-known except for those of the European Shag, *P. aristotelis* (Potts 1971), and the Blue-eyed Shag, *P. atriceps,* including *P. "albiventer"* (Bernstein and Maxson 1981; Rasmussen, in press). Neither of these species is considered closely related to the Rock Shag (Voisin 1973; Siegel-Causey 1986).

The Rock Shag is the only cormorant for which two distinct sequential immature plumages attained by molt have been described (Murphy 1936). Alternate plumages of several cormorant species differ to some degree from basic plumages (e.g., the Long-tailed Cormorant, *P. africanus*; the Blue-eyed Shag; the Spotted Shag, *P. punctatus*; and the Red-faced Cormorant, *P. urile*; Tuck 1978, Harrison 1983). The Rock Shag has been considered to show the greatest difference between basic and alternate plumages of any cormorant species.

Results of field work on austral South American cormorants indicate that confusion exists in the literature regarding molts and plumages of the Rock Shag. This paper provides data on molts of this species, documents that what had been interpreted as two sequential immature plumages is actually geographic variation in phenotype of the juvenal plumage, shows that the winter plumage is not distinct in aspect from the breeding plumage, and demonstrates that adults from the Atlantic coast frequently show a plumage variant rare on the Pacific coast.

METHODS

Numbers, age classes, and localities of Rock Shag specimens examined for molt and juvenal plumage phase are given in Table 1, and localities are shown in Figure 1. I considered specimens to be juveniles if no juvenal feathers had been molted; subadults when molting from juvenal to first basic plumage; and adults when completely in definitive plumage with no retained juvenal feathers. Because the stepwise molt of cormorants results in feathers of varying ages being present at the same time, the following molt scoring system was used for flight feathers: (0) juvenal; (1) missing; (2) feather emerging; (3) to one-fourth grown; (4) to one-half grown; (5) to nearly full-grown; (6) no wear or fading; (7) little wear or fading; (8) light but obvious wear and fading; (9) moderate wear and fading; and (10) heavy wear and fading. Areas of the body plumage examined for molt were head (nape and upper throat to face); neck; back (from top of mantle to rump); venter (from upper breast to vent); scapulars; and tertials. Juvenal-plumaged specimens were

[1] Received 20 October 1986. Final acceptance 16 March 1987.

TABLE 1. Specimens of the Rock Shag examined for molt and juvenal plumage phase.

	Juveniles	Subadults	Adults	Totals
Season				
Winter (Jun–Aug)	2	1	2	5
Spring (Sep–Nov)	3	4	2	9
Summer (Dec–Feb)	27	20	15	48
Fall (Mar–May)	12	2	11	25
Number molting	0	23	23	37
Locality				
Non-Fuegian Argentina	21	8	3	32
Tierra del Fuego	7	0	7	14
Falkland Islands	3	6	8	17
Non-Fuegian Chile	13	13	12	24
Total specimens	44	27	30	101

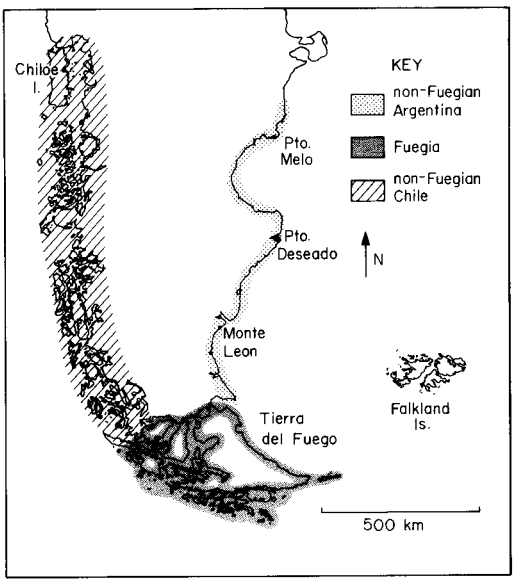

FIGURE 1. Localities given in text, and general areas of the breeding range of *P. magellanicus* in the Fuego-Patagonian region of Argentina and Chile.

classed into five ventral feathering types (Table 2). Adventitious white feathering refers to white areas on the head and neck other than on the cheek or chin.

RESULTS

Primaries of adult and subadult Rock Shags are molted by continual stepwise molt (Stresemann and Stresemann 1966); the first prebasic molt of primaries (PB1) commences at P1 (primary nearest carpal joint) and proceeds peripherally. Before completion of PB1, another wave begins at P1 and proceeds peripherally. The molt of secondaries of subadult and adult Rock Shags is by bidirectional stepwise molt, as in *P. atriceps* (Rasmussen, in press). PB1 molt starts in the most proximal (S15) and most distal (S1) secondaries. Before completion of PB1, PB2 commences at the most distal and most proximal secondaries. Some irregularities occur, but they do not change the general pattern. In secondaries of both wings of three specimens the distal wave of PB1 started before the proximal wave, but in three others, the proximal started first in both wings. Molt data for remiges and rectrices are quantified in Table 3. Molt of rectrices appeared to be irregular in both subadults and adults.

Body molt in three subadult specimens had begun by December, when each was probably no more than 1 year old. PB1 of contour feathers began at about the same time in all body areas examined. I found no evidence for a molt of juvenal feathers of the venter into a second predefinitive plumage; juvenal feathers of the venter were replaced by definitive feathers. Down-tipped head feathers occurred on some specimens with

TABLE 2. Ventral plumage type (from Fig. 2) of specimens and photographs of juvenal Rock Shags, and number of specimens not molting venter feathers.

	Non-Fuegian Chile	Tierra del Fuego	Non-Fuegian Argentina	Falkland Islands	No. not molting
A. Venter pure or almost pure white	6	0	0	0	6
B. Venter with a few dark tips to one-fourth dark	15	3	1	0	11
C. Venter with about half the feathers dark-tipped	1	2	5	4	8
D. Venter with about three-fourths feathers dark-tipped	1	3	10	2	4
E. Venter with no white-tipped feathers	1	1	5	2	5

All localities separately: $G_H = 50.9$, df = 12, $P < 0.001$, G-statistic, Sokal and Rohlf 1981. Chile vs. other localities pooled: $G_H = 48.9$, df = 4, $P < 0.001$.

TABLE 3. Summary of molt data for flight feathers of the Rock Shag; number in parentheses = *n*.

	Subadults	Adults
Primaries		
No. waves per wing	—	$\bar{x}$ = 1.83 ± 0.78 (23) range = 1–3
No. specimens with bilateral symmetry in molt	6 (10)	4 (12)
No. molting primaries per molting wing	$\bar{x}$ = 1.87 ± 0.74 (15) range = 1–3	$\bar{x}$ = 1.68 ± 0.65 (50) range = 1–3
No. molting primaries per molting wave	$\bar{x}$ = 1.65 ± 0.79 (17) range = 1–3	$\bar{x}$ = 1.42 ± 0.57 (54) range = 1–3
Secondaries		
No. waves per wing	—	$\bar{x}$ = 2.0 ± 1.04 (12) range = 1–4
No. specimens with bilateral symmetry in molt	0 (11)	0 (12)
No. molting secondaries per molting wing	$\bar{x}$ = 2.27 ± 1.19 (11) range = 1–4	$\bar{x}$ = 2.65 ± 1.14 (40) range = 1–5
No. molting secondaries per molting wave	$\bar{x}$ = 1.37 ± 0.50 (19) range = 1–2	$\bar{x}$ = 1.31 ± 0.49 (74) range = 1–3
Rectrices		
No. specimens with bilateral symmetry in molt of rectrices	1 (7)	1 (7)
No. molting rectrices per molting tail	$\bar{x}$ = 4.0 ± 1.58 (9) range = 2–6	$\bar{x}$ = 2.4 ± 1.65 (10) range = 1–5

dark ventral feathering as well as those with white (Figs. 2A–E). Juvenal specimens from non-Fuegian Chile usually had white venters, while most non-Fuegian Argentine and Falkland specimens were dark ventrally; Fuegian specimens were more variable than those from farther north on either coast, although no Fuegian specimens had pure white venters (Table 2).

Figure 3 shows seasonality of molt for subadult and adult Rock Shags. The presence of an alternate plumage of head and neck is inferred from two molting adult specimens (SDNHM 38273 and LSUMZ 69634) collected on 9 August and 18 July, respectively.

There is no evidence for a molt into a phenotypically distinct "winter" plumage in the Rock Shag. Nine adult specimens (from the Falklands) with adventitious white feathering scattered on the head and neck (Fig. 4A) were not molting any feathers in those areas (Table 4). In addition, the adventitious white feathering cannot be explained as a result of molt pauses, because many of the feathers involved are parti-colored black and white. I examined 16 adult specimens collected during the austral fall and winter (April through August); 14 of these had black necks and throats as in the breeding plumage (Fig. 4B). The exceptions (LSUMZ nos. 69633 and 69634) had scattered white feathers on the throat and ventral neck. I have seen no fall or winter Rock Shag specimens with the throat and ventral neck entirely or nearly white.

All but two Rock Shag specimens examined with adventitious white feathering were collected in non-Fuegian Argentina and in the Falkland Islands. Two specimens from non-Fuegian Chile (AMNH 443181 and CMNH 123547) have a trace of white on the neck; no Fuegian specimens examined have these irregular markings, and of the scores of adults P. S. Humphrey and I saw in January and February of 1986 in the Beagle Channel at Ushuaia, Tierra del Fuego, none had adventitious white feathering (Table 5).

DISCUSSION

Molts of all flight feathers and body regions in the Rock Shag are like those of other cormorants studied (Potts 1971; Berry 1976; Bernstein and Maxson 1981; Ginn and Melville 1983; Rasmussen, in press). No more than three molt waves occur per primary row; in this respect the Rock Shag is more similar to the Great Cormorant, *P. carbo,* and the European Shag, *P. aristotelis* (Ginn and Melville 1983), than to the Blue-eyed Shag, *P. atriceps* (Rasmussen, in press), which often has four molt waves per primary row.

I found no evidence indicating that there are two immature plumages attained by molt, even

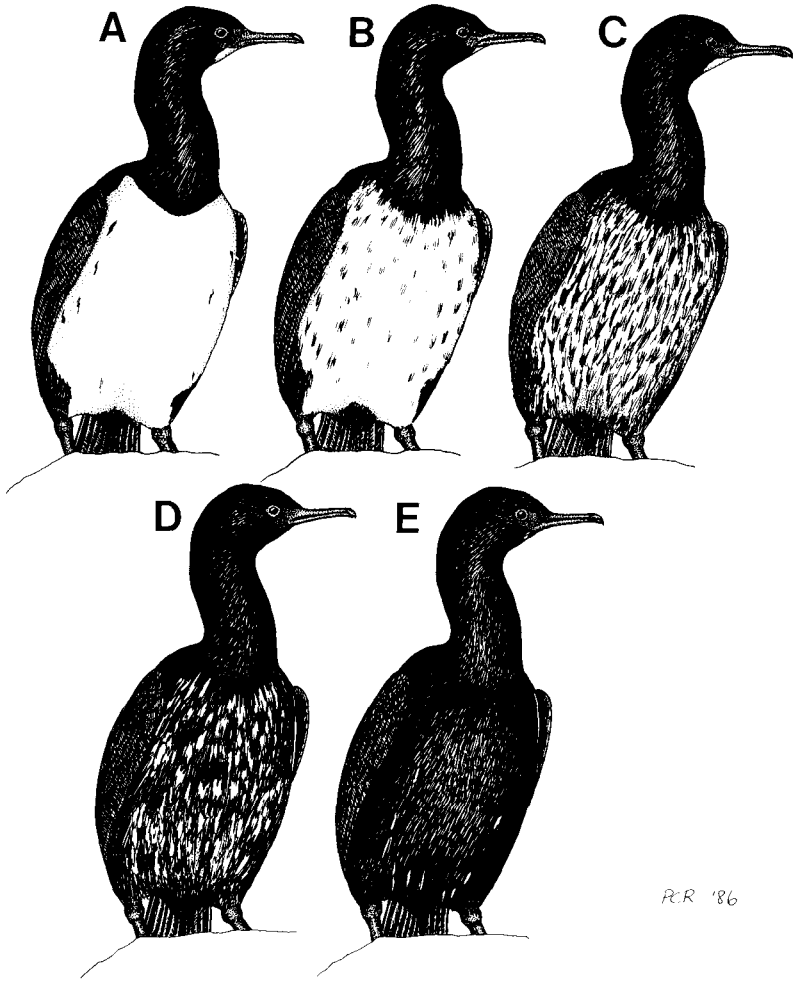

FIGURE 2. Ventral plumage feathering types into which juvenal Rock Shages were classified. A = nearly or completely white; B = about ¾ white; C = about half white; D = about ¾ dark; E = nearly or completely dark. White chin feathering varies independently of ventral plumage type.

though Murphy's (1936) description of the immature plumage sequence states that the first immature plumage, which is white-bellied, molts into a dark-bellied stage; then this second immature plumage molts into another white-bellied stage, the adult plumage. In actuality, there is only one predefinitive (immature) plumage, which varies from totally white on the venter to totally black (Table 2). Many specimens in classes B–D (Fig. 2) were not molting venter feathers (Table 2), and in addition, had some individual feathers of the venter parti-colored dark and white (giving the appearance of a mixture of old and new feathers); therefore these specimens cannot represent intermediate plumage stages. P. S. Humphrey and I have seen only two mostly white-bellied juveniles (as in Fig. 2B) among the scores of nondowny nestlings and fledglings observed at each of the following Argentine localities: Puerto Melo, Chubut Province, and Puerto Deseado and Monte León, Santa Cruz Province (the latter is where the two Atlantic coast specimens in class B were collected). The only juvenile specimens with totally white bellies (Fig. 2A) are those from non-Fuegian Chile, where most juveniles of the sample are white-bellied or nearly so (Table 2). The Atlantic and Pacific populations thus differ greatly in frequency of the

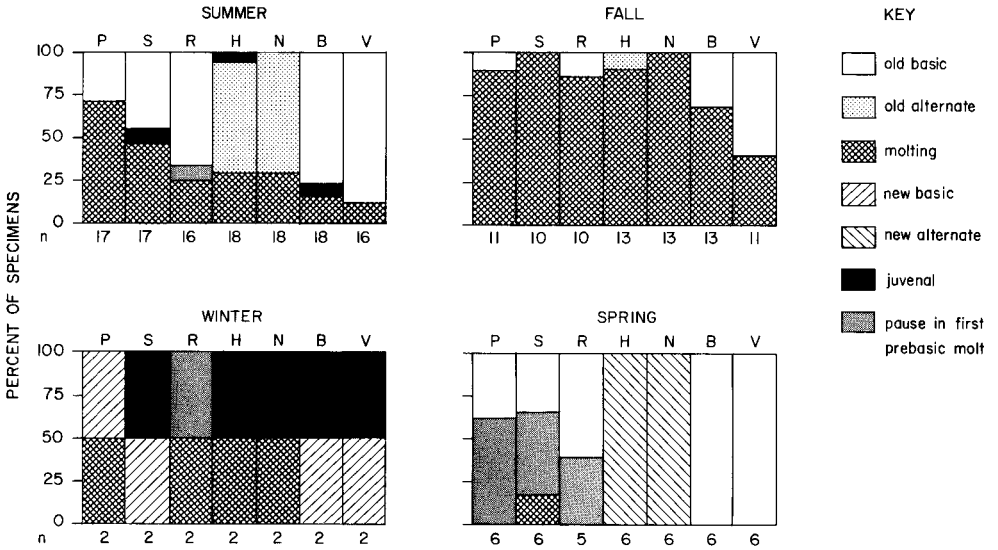

FIGURE 3. Percent of subadult and adult specimens of the Rock Shag in molt and in various plumages for each season. P = primaries, S = secondaries, R = rectrices, H = head, N = neck, B = back, V = venter.

juvenal plumage classes, and in the Fuegian region juveniles tend to be intermediate and more variable.

The Rock Shag is placed in the clade *Sticto-carbo* (Siegel-Causey 1986), in which the juvenal plumage of other clade members (the Pelagic Cormorant, *P. pelagicus,* and the Red-faced Cormorant) is dark below, as it is in most other cormorants. Another member, the Red-legged Shag (*P. gaimardi*), often has a dark gray venter in the juvenal plumage (Rasmussen, unpubl. data). Thus the white-bellied juvenal plumage is best considered derived where it occurs in Rock Shags. It is likely that this plumage variant arose during separation of the Atlantic and Pacific populations of this species caused by Llanquihue Glaciation from 20,000 ybp to 10,000 ybp (Mercer 1976). In this vicariance event, the marine littoral was uninhabitable from just south of Chiloé Island, Chile (Flint 1971), to Tierra del Fuego, excluding the eastern Fuegian region (Porter et al. 1984). During this time the presumably small, isolated Pacific population of the Rock Shag occupying the Chiloé refugium may have been affected by the founder effect or genetic drift. Following glacial retreat, repopulation of southern Chile and subsequent mixing in the Fuegian region of the two formerly isolated populations may explain the intermediacy in juvenal plumage classes from that area relative to Atlantic and Pacific populations. The only two nearly white-bellied juvenal specimens (Fig. 2B) from the Atlantic coast were collected at Monte León; this and preliminary evidence from *P. atriceps*

TABLE 4. Molt condition and extent of white in Rock Shags from the Falkland Islands (AMNH Beck collection).

Specimen no.	Date	Molt on head, neck	Adventitious white feathering
443219	10 Jan	None, none	Numerous white feathers in lower throat.
443209	10 Dec	None, none	Entire throat and crest mostly white.
443208	16 Dec	None, none	Ventral neck largely white.
729946	2 Jan	None, none	Some white feathers in lower throat.
443218	10 Jan	None, none	Entire throat mostly white, scattered white feathers elsewhere.
443202	17 Dec	None, none	Entire throat mostly white, crest mostly white.
446191	10 Dec	None, none	Entire throat mostly white, crest mostly white.
443206	4 Nov	None, none	Entire throat mixed black and white.
443207	4 Nov	None, none	Few white feathers in central throat.

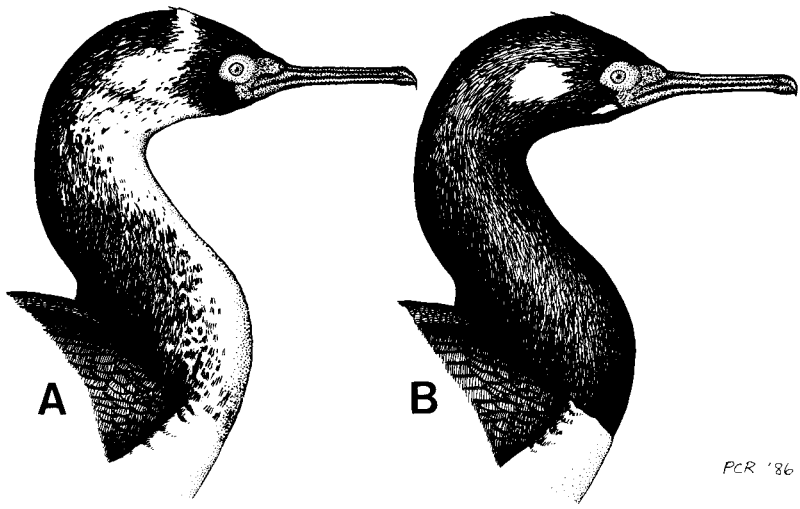

FIGURE 4. Head and neck of A: typical mottled breeding plumage specimen (AMNH 443202; 17 December; head and neck not molting); B: winter-plumaged specimen (SDNHM 38273; 7 August). A is in basic plumage, B is in combined alternate and basic plumages.

(specimens spanning the size range of this otherwise highly clinal species occur at Monte León in the breeding season; Rasmussen, unpubl. data) suggest that the Monte León area is currently a zone of mixing between Fuegian and more northerly Patagonian cormorant populations.

Other cormorants known to have polymorphic juvenal plumages are the Pied Cormorant, *P. varius,* the Little Pied Cormorant, *P. melanoleucus,* the Stewart Island Cormorant, *P. chalconotus* (adults also polymorphic in the latter two forms), and the Kerguelen Shag, *P. verrucosus* (Falla 1937, Falla et al. 1966, Voisin 1973, Harrison 1983). The Rock Shag is not usually considered closely related to any of these species (Siegel-Causey 1986), although Falla (1937) and Voisin (1973) postulated relationship between Rock and Kerguelen cormorants on the basis of plumage characters.

The adventitious white feathering around the head and neck found on many breeding specimens of the Rock Shag was explained by Murphy (1936) as an intermediate stage between breeding and nonbreeding plumages. However, I found that none of the AMNH Beck collection specimens on which he based this opinion were molting feathers of the head or neck. The lack of white-necked winter museum specimens and the occurrence of at least 15 black-necked winter-collected specimens (and two with white speckling) in U.S. museums also argue against Murphy's interpretation. Harrison (pers. comm.) based his 1983 illustration of the "winter-plumaged" Rock Shag on Murphy's description, as apparently have others. All evidence shows that there is no phenotypically distinct winter plumage in the Rock Shag, and that adults with adventitious white feathering are merely plumage

TABLE 5. Numbers of specimens examined and sight records of individuals with adventitious white feathering on head and neck.

Locality	No. adult phenotype specimens examined	No. specimens with adventitious white feathering	Sightings and photos of individuals with adventitious white feathering
Pto. Melo, Argentina	16	2	several
Pto. Deseado, Argentina	17	1	several
Monte León, Argentina	7	2	several
Falkland Islands	11	8	several
Tierra del Fuego	28	0	none
Non-Fuegian Chile	20	2 (very few whites)	none

variants similar to those that occur in the Bank Cormorant, *P. neglectus* (Harrison 1983), rather than a transitional stage between plumages. There apparently is an alternate plumage of the head and neck in the Rock Shag, but more specimens are needed to verify this. The Blue-eyed Shag, the European Shag, and the North American cormorants all have an alternate plumage of the head and neck (Palmer, in litt.). Winter Rock Shag specimens (Fig. 4B) are very similar in aspect to summer specimens but have more highly developed filoplumes on the head, back, wing coverts, and thighs; these filoplumes are probably the supplemental feather generation, as in other cormorants (Palmer, in litt.).

Rock Shags with adventitious white feathering, while frequent in non-Fuegian Argentina and the Falkland Islands, are unknown from Fuegia and rare in non-Fuegian Chile. This, in addition to differential distribution of juvenal plumage classes, supports evolution in isolation by this relatively sedentary species. Because of lowered sea levels, the unglaciated Falkland Islands (Muller 1973) were separated from mainland Atlantic Patagonia by much narrower straits during the Llanquihue Glaciation than at present (Fray and Ewing 1963, Flint 1971), and thus Rock Shags in the Falklands would not have been as isolated from the main Atlantic population as was the population in the Chiloé refugium. In this species, therefore, geographic proximity during a major vicariance event is congruent with degree of plumage differentiation.

ACKNOWLEDGMENTS

This study would not have been possible without many kinds of assistance from P. S. Humphrey and D. Siegel-Causey. For information, loan of specimens, and access to collections I thank G. E. Barrowclough, W. E. Lanyon, and M. LeCroy (American Museum of Natural History [AMNH]); K. C. Parkes (Carnegie Museum of Natural History [CMNH]); R. Schreiber (Los Angeles County Museum); J. V. Remsen, Jr. (Louisiana State Museum of Zoology [LSUMZ]); R. Paynter (Museum of Comparative Zoology [MCZ]); J. Navas (Museo Argentino de Ciencias Naturales); R. L. Zusi (National Museum of Natural History); A. Rea (San Diego Natural History Museum [SDNHM]), and E. Stickney (Yale Peabody Museum). P. Harrison provided helpful information. R. S. Palmer and M. Gottfried read and improved the manuscript. For permits, lodging, and other assistance, I thank B. Mayer and F. Fauring, Patagonia Comercial S. R. L.; C. O. Perez, Ministerio de Economía, Chubut; J. Vinuesa and C. Schroeder, Centro Austral de Investigaciones Científicas; R. Clarke, Dpto. Conservación de la Fauna, Santa Cruz Province; and R. Cerezani, Dirección de Recursos Naturales, Territory of Tierra del Fuego, Argentina. This study was supported by the Frank M. Chapman Memorial Fund and the American Museum of Natural History Collections Study Grant Program; the Museum of Natural History and the Department of Systematics and Ecology, University of Kansas, and the Kansas University Endowment Association; the Humphrey family; and National Science Foundation Grant BSR-8407365 to Humphrey and Siegel-Causey.

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