MOULTS OF RECTRICES AND BODY PLUMAGE OF BLUE-EYED AND KING SHAGS (*Phalacrocorax atriceps* AND *P. albiventer*) AND PHENOLOGY OF MOULTS

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ABSTRACT

In Blue-eyed and King Shags (*Phalacrocorax atriceps* and *P. albiventer*), moult of the rectrices is irregular but not random. R1 (Rectrix 1) was usually the first to be replaced in subadult Blue-eyed Shags but not in adults. In Blue-eyed Shags, moulting rectrices were most often separated by one or two non-moulting rectrices. When two adjacent rectrices were moulting in adult Blue-eyed Shags, one was usually over half grown before the other began moulting, or both were about the same length or missing. Up to six rectrices moult simultaneously in subadults and up to eight in adults. Moult of rectrices is usually not symmetrical in Blue-eyed Shags. In adults, the number of moulting feathers and the number of waves are correlated among flight feathers. In flight feathers of subadults, the number of moulting feathers is not correlated but the number of moulting waves and the number of retained juvenile flight feathers are correlated. Most moult of flight and body feathers takes place after breeding, but a limited amount occurs during breeding and in winter.

INTRODUCTION

Cormorants (Phalacrocoracidae) are one of the few groups of birds that, in addition to undergoing a heavy prebasic moult into basic (non-breeding) plumage in the late summer and early autumn, moult to a limited extent during breeding and in winter (Witherby *et al.* 1940; Falla 1932; Stead 1932; Turbott 1956; Rand 1960; Palmer 1962; Potts 1971; Watson 1975; Berry 1976; Bernstein & Maxson 1981; Crawford *et al.* 1982; Ginn & Melville 1983; Cooper 1985; Rasmussen in press *a*, in press *b*).

Primaries moult by continual stepwise moult ("*Staffelmauser*", Stresemann & Stresemann 1966; "serially descendent moult", Ginn & Melville 1983). Several authors have suggested that stepwise moult of primaries allows slow moult and thus permits limited moult during stressful times (*i.e.* winter and breeding). However, most cormorants moult body and tail feathers as well as remiges during breeding, and it is not clear how stepwise moult of remiges makes moult of other feather groups any less stressful.

No detailed analyses of moult of rectrices in cormorants have been published. Moult of rectrices is said to be irregular in cormorants by some investigators (Owre 1967, Berry 1976, Cramp & Simmons 1977, Bernstein & Maxson 1981), or centripetal and alternating (Verheyen 1953, Crawford *et al.* 1982). Stresemann & Stresemann (1966) stated that cormorants tend to moult rectrices alternately, and that a 1-6-4-2-3-5 pattern of tail moult is typical of members of the family. Other pelecaniforms are thought to have irregular moult of rectrices as well (Gurney 1913, Dorward 1962, Stonehouse 1962, De Korte & De Vries 1978, Nelson 1978*a*, *b*).

Blue-eyed and King Shags (*Phalacrocorax atriceps* and *P. albiventer*) are large black and white cormorants, each represented by several subspecies, in southern South America, the Falkland Islands, the Antarctic Peninsula, the Prince Edward Islands, Marion Island, the Crozet Islands, Heard Island, South Georgia, and Macquarie Island (Murphy 1916, 1936; Behn *et al.* 1955; Watson *et al.* 1971; Watson 1975; Devillers & Terschuren 1978; Williams & Burger 1979). These probably conspecific (Devillers & Terschuren 1978, Rasmussen 1986) cormorants have moult of primaries that appears irregular (Murphy 1916), but occurs by stepwise moult (Bernstein & Maxson 1981, Rasmussen in press *b*), as is typical of cormorants (Stresemann & Stresemann 1966). The first prebasic (post-juvenile) moult (PB1, Humphrey & Parkes 1959) begins at Primary 1 (P1) and proceeds distally; stepwise moult begins when PB2 starts before the completion of PB1 (Rasmussen in press *b*). Adult Blue-eyed Shags have up to four concurrent waves of moult in primaries. Secondaries are moulted by bidirectional stepwise moult; waves of PB1 begin at the distal- and proximal-most secondaries and move centrally, and then PB2 begins distally and proximally before completion of PB1. There are up to six concurrent waves in moult of secondaries. Remiges are usually moulted asymmetrically, and subadults have more moulting feathers per wave than do adults (Rasmussen in press *b*). Bernstein & Maxson (1981) found that for the Antarctic Blue-eyed Shag all feather tracts moulted at their heaviest from the end of March to mid-April, and that moult of rectrices was "irregular and often unilateral."

This account provides information on the characteristics of moult of rectrices; seasonality of moult; and degree of correlation of moult among major feather groups for subadult and adult Blue-eyed and King Shags.

METHODS

Specimens which had not yet begun PB1 (the first prebasic moult) were considered juveniles; specimens in PB1 subadults; and specimens which no longer had any juvenile feathers adults. Sample size is given in Table 1. The sample size of King Shags was too small to permit certain of the quantitative analyses which were done for Blue-eyed Shags.

Primaries were numbered P1 (Primary 1) to P10 proximally to distally, secondaries S1 (Secondary 1) to S15 distally to proximally, and rectrices R1 (Rectrix 1) to R6 medially to laterally. I took relative age and moult data from as many flight feathers of each specimen as possible. Age categories 0-10 (1-5 are also growth categories) were assigned to each flight feather: (0) juvenile; (1) missing; (2) new feather just visible; (3) less than ¼ grown; (4) ¼ to ½ grown; (5) greater than ½ to not quite fully grown; (6) full-length, no wear or fading; (7) very slight wear and/or fading; (8)

light but obvious wear and fading; (9) moderate wear and fading; (10) heavy wear and fading. For justification of this method, see Rasmussen (in press *b*).

TABLE 1 — Number and nature of specimens of Blue-eyed and King Shags examined for each season, age, and locality

	Blue-eyed	King
Season		
Winter (Jun-Aug)	4	9
Spring (Sep-Nov)	10	10
Summer (Dec-Feb)	60	39
Autumn (Mar-May)	23	10
Ages		
Juveniles	14	17
Subadults	33	20
Adults	50	31
Locality		
South America	51	48
Falkland Is.	0	15
South Georgia I.	10	0
Shag Rocks (50°33'S, 43°02'W)	1	0
South Shetland Is.	17	0
Antarctica	18	0
Macquarie I.	0	5
Nature of specimens		
Museum skin	70	60
Freshly collected	27	8
Totals	97	68

To determine which (if any) rectrices tended to be replaced first, I tallied frequency of being first-replaced for each rectrix number from R1 to R6 of the left side of the tail (or the right if the left was not usable). For two-way ties between earliest-replaced rectrices within a tail, each was tallied as 0.5; for three-way ties, 0.33; and four-way ties, 0.25. A chi-square analysis was done using equal expected frequencies.

I considered moult of rectrices completely symmetrical if feathers of each bilateral pair (L5, R5) were in the same age category or were moulting simultaneously. Individual rectrix pairs were symmetrical if both feathers of the bilateral pair were in the same age category or were moulting simultaneously.

I examined moult of the following body regions: head (from chin and nape up); neck (from below chin and nape to top of breast and mantle); back (mantle to rump); venter (breast to vent); tertials; and scapulars. Categories describing amount of moult of each body region were: (0) none; (1) very light; (2) light; (3) moderate; (4) heavy. Intensity of moult for body regions was defined as the average of these categories for each region, and for flight feathers, intensity was the average number of moulting feathers per side of each specimen.

To determine predictability of moult among feather groups, Pearson's product-moment correlations were done on the number of moulting feathers on the left wing of each specimen for primaries and secondaries, the left side of each specimen for rectrices, and the presence of body moult.

RESULTS

Moult of rectrices

No regular sequence of replacement could be determined by inspection of rectrix moult data for Blue-eyed and King Shags. In subadult Blue-eyed Shags, R1 is usually the first replaced (X^2=32.12, df=5, $P < 0.001$, Figure 1). In adult Blue-eyed Shags there was no discernible pattern.

Subadult and adult Blue-eyed Shags were very similar in number of non-moulting rectrices occurring between pairs of moulting rectrices (Figure 2). Most pairs of moulting rectrices were separated from each other by one or two non-moulting rectrices in both age classes.

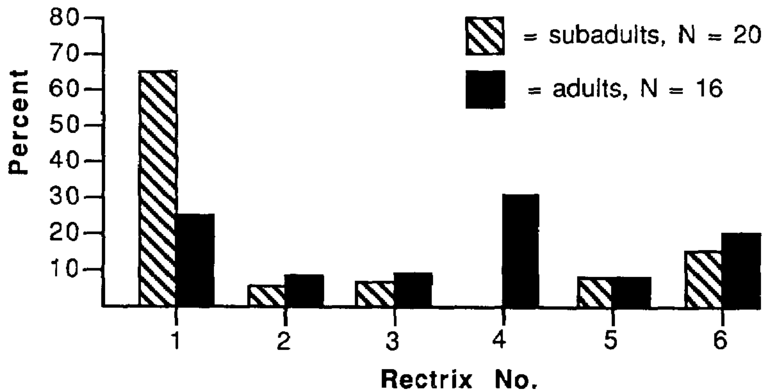

FIGURE 1 — Percentage of cases in which each rectrix was replaced first in subadult and adult Blue-eyed Shags

Adjacent moulting pairs of rectrices in adult Blue-eyed Shags tended to differ by either zero or three growth categories (Figure 3). The earlier-moulted rectrix was more than half-grown before loss of the adjacent rectrix in 50% of the adult Blue-eyed Shags. Of 37 adult King Shags only six had adjacent rectrix pairs that were moulting simultaneously. In most, rectrices were moulted singly (Figure 4); subadults rarely moulted up to four adjacent rectrices simultaneously; adult Blue-eyed Shags up to five; and adult King Shags only up to three adjacent rectrices simultaneously.

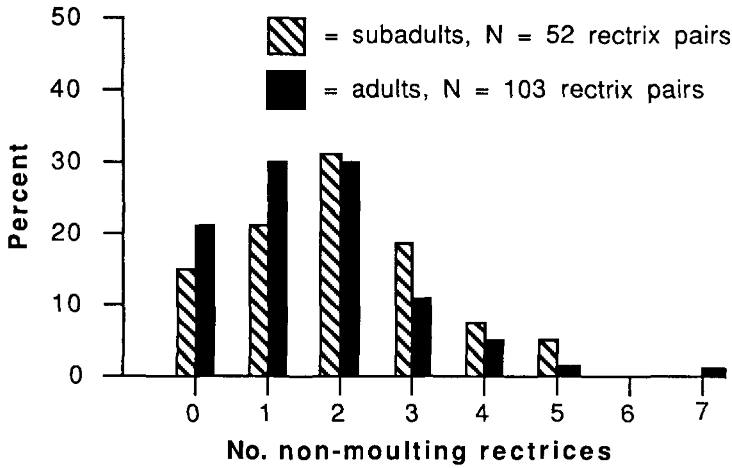

FIGURE 2 — Number of non-moulting rectrices between pairs of moulting rectrices in subadult and adult Blue-eyed Shags

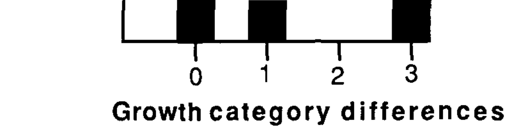

FIGURE 3 — Differences in growth categories between adjacent moulting pairs of rectrices in adult Blue-eyed Shags

In subadult Blue-eyed Shags, the number of moulting rectrices per tail was $\bar{x}$ = 3.70, s.d. = 1.76, range = 0-6, n = 17; in adults, $\bar{x}$ = 3.04, s.d. = 2.3, range = 0-8, n = 44. In subadult King Shags, the number of moulting rectrices per tail was $\bar{x}$ = 2.91, s.d. = 2.34, range = 0-6, n = 11; in adults $\bar{x}$ = 2.5, s.d. = 2.4, range = 0-7, n = 35. Adults more frequently were not moulting rectrices, and sometimes moulted more rectrices simultaneously than subadults (Figure 5).

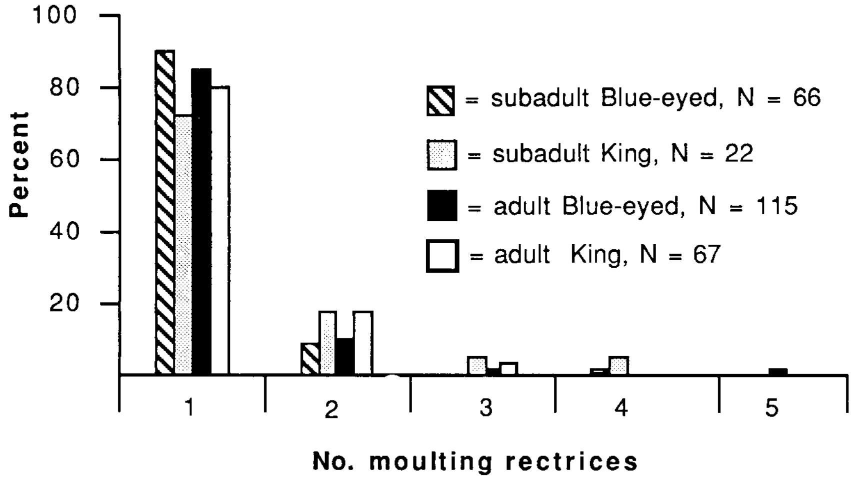

FIGURE 4 — Number of adjacent rectrices moulting in subadult and adult Blue-eyed and King Shags. 1 = rectrices moulting singly

Symmetry of moults

Seven of 21 subadult Blue-eyed Shag specimens had completely symmetrical moult of rectrices, but none of 31 adult Blue-eyed Shags and 17 King Shags had complete symmetry of moult of rectrices. Of 53 bilateral rectrix pairs in subadult Blue-eyed Shags, moult was symmetrical in 23 pairs (43%), and of 113 bilateral rectrix pairs in adult Blue-eyed Shags, moult was symmetrical in 26 pairs (23%). Of 102 bilateral rectrix pairs in adult King Shags, moult was symmetrical in 44 pairs (43%). Differences between subadult and adult Blue-eyed Shags were not statistically significant (complete symmetry: $X^2 = 1.35$, df = 1, $P > 0.05$; bilateral symmetry: $X^2 = 1.30$, df = 1, $P > 0.05$).

Correlation of moults

The number of moulting primaries was not correlated with the number of moulting secondaries, nor was the number of moulting remiges correlated with the number of moulting rectrices in subadults of either form (Table 2). The number of moulting feathers per primary row was significantly correlated with the number of moulting feathers per secondary row in adult Blue-eyed and King Shags. The number of moulting waves in primaries of Blue-eyed Shags and adult King Shags was significantly correlated with the number of moulting waves in secondaries, but was not correlated in 15 subadult King Shags. The number of juvenile primaries remaining was strongly correlated with the number of juvenile secondaries in subadult Blue-eyed and King Shags. The number of juvenile remiges remaining was strongly correlated with the number of juvenile rectrices in subadult Blue-eyed Shags but not in subadult King Shags.

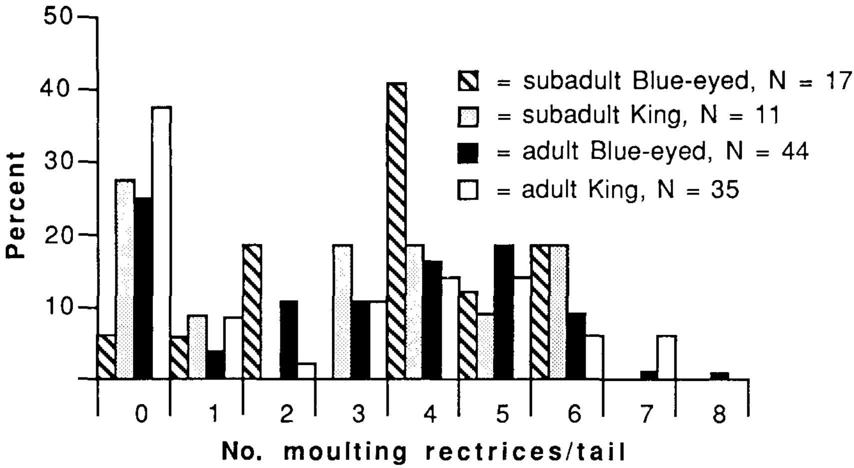

FIGURE 5 — Number of rectrices moulting per tail in subadult and adult Blue-eyed and King Shags

TABLE 2 — Correlations between moult of selected body regions for Blue-eyed and King Shags

	Blue-eyed Shag				King Shag			
	Subadult		Adult		Subadult		Adult	
Correlation	*r*	*n*	*r*	*n*	*r*	*n*	*r*	*n*
No. moulting primaries vs. secondaries	0.29	27	0.50**	40	0.17	15	0.66**	30
No. moulting remiges vs. rectrices	0.09	25	0.78**	36	0.37	15	0.80**	31
No. moulting waves in primaries vs. secondaries	0.56**	26	0.52**	40	0.37	15	0.58**	31
No. remaining juvenile primaries vs. secondaries	0.77**	27	—	—	0.95**	16	—	—
No. retained juvenile remiges vs. rectrices	0.70**	25	—	—	0.24	15	—	—

*=$P<0.05$;**=$P<0.01$.

TABLE 3 — Number of specimens moulting in selected feather groups but not in other specified groups for Blue-eyed and King Shags. Number examined for each category is in parentheses

	Blue-eyed Shag		King Shag	
	Subadult	Adult	Subadult	Adult
No. moulting primaries but not secondaries	12 (28)	6 (37)	4 (15)	6 (30)
No. moulting secondaries but not primaries	1 (28)	5 (37)	4 (15)	0 (30)
No. moulting remiges but not rectrices	2 (25)	5 (36)	4 (15)	3 (30)
No. moulting rectrices but not remiges	0 (25)	0 (36)	0 (15)	1 (30)
No. moulting remiges but not body feathers	3 (27)	5 (29)	4 (17)	5 (19)
No. moulting body feathers but not rectrices	2 (23)	5 (22)	2 (13)	4 (19)
No. moulting rectrices but not body feathers	1 (23)	2 (22)	3 (13)	2 (19)
No. moulting body feathers but not flight feathers	2 (27)	0 (29)	4 (17)	0 (19)
No. commencing PB1 in primaries before secondaries	22 (25)	—	12 (13)	—
No. commencing PB1 in secondaries before primaries	2 (25)	—	0 (13)	—

In both age classes of both species, moult occurred in several cases in primaries when secondaries were not moulting (Table 3). Subadult Blue-eyed Shags and adult King Shags rarely moulted secondaries when not moulting primaries. All classes infrequently moulted remiges when not moulting rectrices and, one exception, did not moult rectrices without also moulting remiges. Most specimens moulted body feathers while moulting remiges and rectrices. Very few subadult specimens and no adults moulted body feathers when not moulting flight feathers.

All feather groups moulted at highest intensity in summer and autumn in subadult and adult Blue-eyed and King Shags (Figure 6). Almost all subadult and adult Blue-eyed Shags were moulting all feather groups (except venter and scapulars) during summer and autumn (Figure 7). In winter a prealternate (pre-breeding) moult of the head and neck occurred in two Blue-eyed Shags and one King Shag. In the two adult Blue-eyed Shags, prealternate moult also occurred in the region of the white back patch, but not elsewhere on the back. No King Shags had prealternate moult on the back.

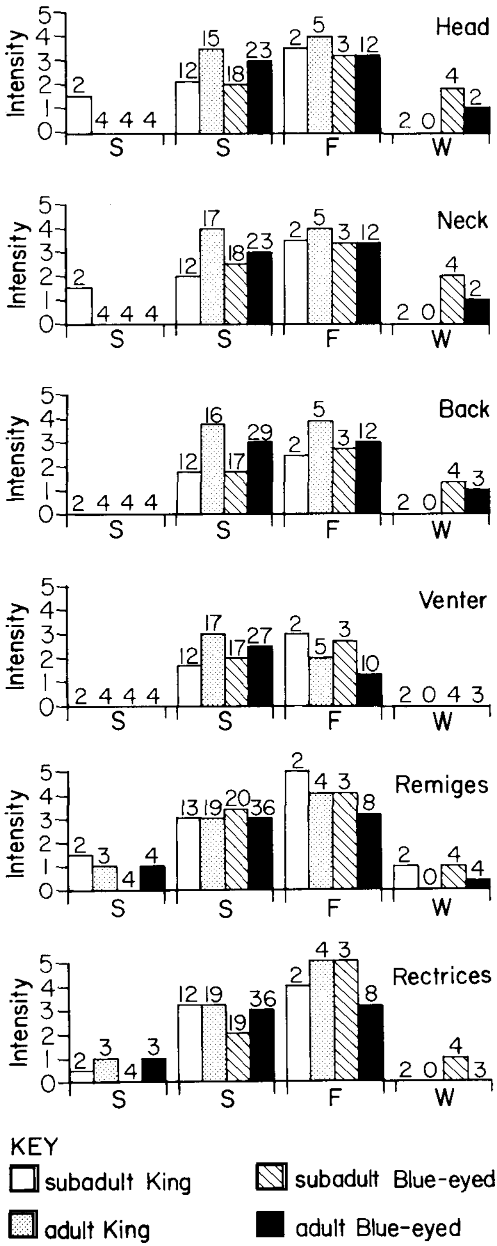

FIGURE 6 — Mean seasonal (austral spring, summer, autumn, winter) moult intensity of various feather groups for subadult and adult Blue-eyed and King Shags. Intensity of moult is defined in the Methods. Number above bar is sample size for that season

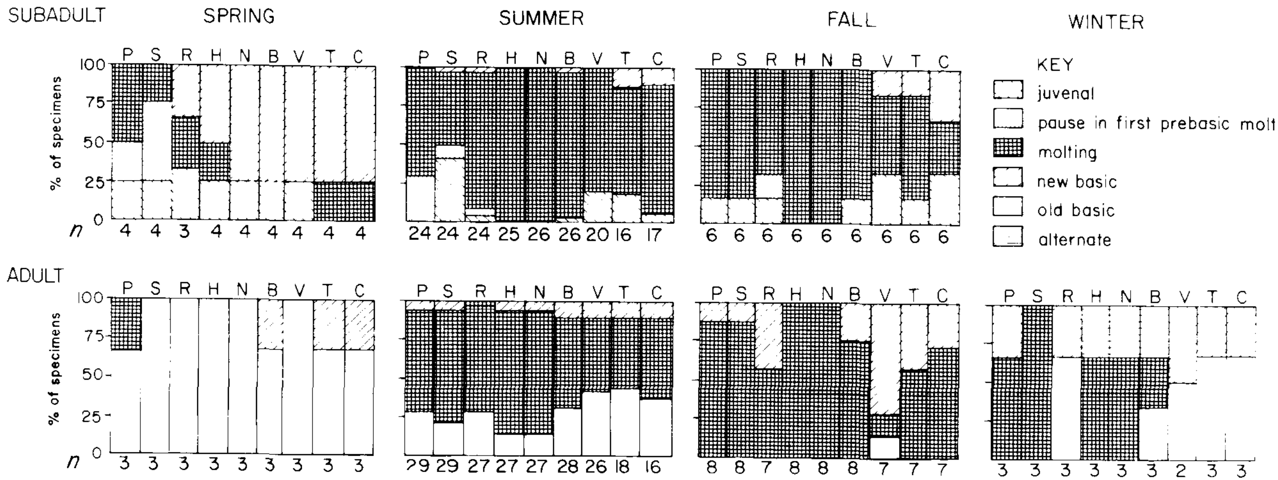

FIGURE 7 — Seasonal percent of adult and subadult Blue-eyed Shag specimens in juvenile, basic, or alternate plumage, or moult of each feather group. No winter specimens of subadult Blue-eyed Shags were available for this study. P. = primaries, S = secondaries, R = rectrices, H = head, N = neck, B = back, V = venter, T = tertials, C = scapulars

Only six adult Blue-eyed Shags were not moulting any feathers when collected (Jan., 2; Aug., 1; Sep., 1; Dec., 2), and only five adult King Shags (Jan., 1; Nov., 1; Dec., 3).

DISCUSSION

Moult of rectrices

In Blue-eyed Shags, moulting rectrices are separated by two or three feathers more often than moulted alternately (Figure 2), although the Cormorant (*P. carbo,* Ginn & Melville 1983) and cormorants as a group tend to moult rectrices alternately (Stresemann & Stresemann 1966). In addition, no Blue-eyed or King Shags showed a pattern of tail moult which conformed to the 1-6-4-2-3-5 sequence that, according to Stresemann & Stresemann (1966), characterises the moult of rectrices in all cormorants.

The pattern of moult of rectrices in Blue-eyed and King Shags, although it at first appears random and unpredictable, actually ensures that few large gaps are present at any one time, even when moult is at its heaviest.

Symmetry of moult of remiges

Moult of rectrices is asymmetrical in Blue-eyed and King Shags as well as in adult Cape Cormorants (*P. neglectus* n = 56, $\bar{x}$ = 17.6% symmetry, raw data from Berry 1976) and Great Frigatebirds (*Fregata minor* n = 16, 31.3% symmetry, raw data from De Korte & De Vries 1978). The minor differences in bilateral symmetry of rectrix moult in adult and subadult Blue-eyed Shags suggest that the pattern is not fixed in an individual throughout life, at least not between the first and succeeding prebasic moults. Moult of remiges also tends to be asymmetrical in Blue-eyed and King Shags (Bernstein & Maxson 1981, Rasmussen in press *b*), as well as in other pelecaniforms.

Intensity and linkage

Body moult of Blue-eyed and King Shags was heaviest in summer and autumn (Figure 6); this agrees with Murphy's (1936) and Watson's (1975) statements that Blue-eyed Shags begin moulting in the breeding season and continue until June: however, this study and Bernstein & Maxson's (1981) study showed that moult occurred at lower intensities at other seasons. In Antarctic Blue-eyed Shags, body moult was heaviest in March and April (Bernstein & Maxson 1981).

The assertion that a post-juvenile (first prebasic) tail moult occurs very soon after fledging in Blue-eyed and King Shags (Murphy 1936) was not supported by this study. The first prebasic moult of rectrices in these species occurs at about the same time as PB1 of remiges and contour feathers (Table 3; Figures 6, 7). Known-age individuals of the King Shag of Macquarie Island (*P. albiventer purpurascens*) attained full adult plumage in their second year of life (Brothers 1985); however, some Antarctic Blue-eyed Shags retained a few juvenile remiges at three years of age (P. Shaw, pers. comm. *in* Bernstein & Maxson 1981).

In addition to the known prealternate moult of the head of Blue-eyed and King Shags and the middle of the back in the Blue-eyed Shag (Watson 1975), a prealternate moult also occurs on the neck (Figure 7). The moults of remiges that occur in winter and spring, because they are continuous (Rasmussen in press *b*), cannot be considered prealternate even though they are concurrent with the prealternate moults of head and neck.

Almost all adult specimens of both forms examined in this study were moulting, several during breeding and winter. Bernstein & Maxson (1981) reported five non-moulting Antarctic Blue-eyed Shags during March, but they apparently included data for juveniles (which do not begin moult until nearly a year old) with those for adults. Nelson (1983) suggested that it should be more advantageous for inshore-feeding pelecaniforms to become stressed in order to produce more young than for pelagic feeders to do so. Although Nelson did not discuss moult as a form of stress, this hypothesis is supported by Stonehouse's (1962) study, in which he found that in pelagic tropicbirds, courtship did not begin until moult was completed (Red-billed, *Phäethon aethereus*), or birds infrequently began breeding with a few moulting feathers (White-tailed, *P. lepturus*). Members of the other pelecaniform families are mostly inshore feeders, and as far as known all moult to some extent during breeding (Gibson-Hill 1950, Rand 1959, Stonehouse 1962, Dorward 1962, Nelson 1964, Bauer & Glutz 1966, De Korte & De Vries 1978, Nelson 1978*a*, *b*).

Although PB1 generally began in primaries before secondaries, and the number of juvenile feathers retained was generally correlated among feather groups in Blue-eyed and King Shags, the number of moulting primaries per specimen was uncorrelated with the number of moulting secondaries; this reflects the variability in number of feathers per wave in subadults.

Adults showed strong correlations in moult among flight feathers, both in number of feathers moulting and in number of moulting waves. In both subadults and adults, when secondaries, rectrices, and/or body feathers were moulting, primaries were usually moulting as well, but primaries frequently moulted when these other feather groups were not moulting. Although data are lacking, it is possible that slower rates of growth of the primaries than of the other flight feathers account for their longer period of moult.

Considerable variability was evident in all aspects of the moult of both Blue-eyed and King Shags, as is the case in other species of cormorants (Potts 1971, Berry 1976, Bernstein & Maxson 1981, Ginn & Melville 1983, and others). This was strikingly shown by two adult female Blue-eyed Shages from Puerto Deseado, Argentina, collected together on the same rock on 22 February 1985; one of these birds had just started moult after a pause while the other had nearly completed body moult and had many new remiges. Some of the variability in moults is related to age, and variability may also be related to breeding success (De Korte & De Vries

1978), sex (Pitts 1971), geographic variation in breeding times (Potts 1967, 1969), individual variation (Dementiev & Gladkov 1951, Nelson 1978), nutritional factors, or lack of selective controls.

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