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STEPWISE MOLT OF REMIGES IN BLUE-EYED AND KING SHAGS[1]

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Abstract. In Blue-eyed and King shags (*Phalacrocorax atriceps* and *P. albiventer*), the first prebasic molt of the primaries begins at P1 and proceeds distally. Continual stepwise molt of the primaries begins with commencement of PB2 after replacement of P5 to P8 by the first prebasic molt. Adults had from one to four concurrent distally moving waves of molt in primaries. In secondaries of these species, the first prebasic molt begins peripherally at S1 and S15 and proceeds centrally. The second prebasic molt then begins peripherally before the central secondaries are replaced by PB1. Secondaries of adults are molted by up to six concurrent waves that originate peripherally; I term this bidirectional stepwise molt of secondaries. Stepwise molt tends to be asymmetrical both in adults and subadults. Subadults of these species have more molting feathers per wave in primaries and secondaries than do adults, but the age classes do not differ in number of molting feathers per wing. Molt of remiges in subadults initially resembles the condition in the Procellariiformes, the nearest outgroup, while the stepwise molt of adults is synapomorphic for Pelecaniformes.

Key words: Blue-eyed Shag; King Shag; Phalacrocorax atriceps; Phalacrocorax albiventer; *molt.*

INTRODUCTION

Although the wing molts of cormorants (Phalacrocoracidae) are highly complex and unusual, detailed information on molts of primaries in this cosmopolitan family is available only for the European Shag (*Phalacrocorax aristotelis*; Potts 1971). All species of Pelecaniformes studied thus far have shown stepwise molt (called "*Staffelmäuser*" by Stresemann and Stresemann 1966, and "serially descendent molt" by Ginn and Melville 1983) of the primaries (Dorward 1962, Potts 1971, Berry 1976, DeKorte and DeVries 1978, Bernstein and Maxson 1981, Crawford et al. 1982, Ginn and Melville 1983, Cooper 1985, Rasmussen 1987). However, very little is known concerning the ontogeny and mode of progression of stepwise molt in primaries. In stepwise molt of primaries, a molt wave begins at a certain point (in most species Primary 1 [P1]) before the previous wave, which originated at the same point, is completed; thus there is more than one concurrent, overlapping molt wave (see Figs. 1A, B). "Continual stepwise molt" occurs in Pelecaniformes and a few other birds (Stresemann and Stresemann 1966); in this type of stepwise molt successive waves begin at P1. Each wave eventually reaches the wing tip (Ashmole 1968), but not during the year in which the wave began (at least not in the Masked Booby, *Sula dactylatra*, Dorward 1962; or the European Shag, Potts 1971). Each wave probably continues from where it paused; primaries are replaced once per year or less in the Masked Booby (Dorward 1962). The other known type of stepwise molt is "periodic stepwise molt" (Stresemann and Stresemann 1966), in which successive waves begin at the innermost primary, but only one of every two, or two of three waves reach the wing tip. A variable number of the outermost primaries are thus molted less frequently than the innermost, although every primary is molted at least once yearly. Periodic stepwise molt is known only in some terns of the genus *Sterna* (Stresemann and Stresemann 1966).

The molt of secondaries in Pelecaniformes has been virtually ignored; published data on molt patterns of secondaries in members of this diverse order exist only for the Rock Shag (*P. magellanicus*; Rasmussen 1987). Few data have been published on molts of the Blue-eyed Shag and the King Shag morph (*P. atriceps* and *P. "albiventer"*; Watson 1975, Bernstein and Maxson 1981). In the Antarctic Blue-eyed Shag (*P. atriceps bransfieldensis*) molt of flight feathers appears irregular, with no obvious orderly sequence of molt (Bernstein and Maxson 1981).

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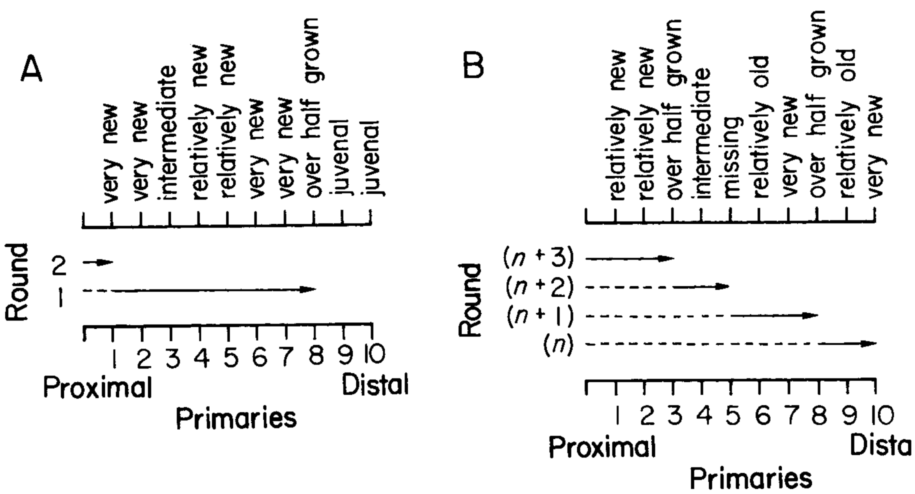

FIGURE 1. Stepwise molt of primaries. Arrows indicate apparent direction and extent of wave progression; dashed portions of arrows indicate feathers of that round presumed replaced by later round(s). (A) Subadult King Shag, YPM 82275; commencement of stepwise molt. (B) Adult Blue-eyed Shag, AMNH 443237; four-round stepwise molt.

In this paper I document the ontogeny of stepwise molt of the remiges in Blue-eyed and King shags, and describe and compare characteristics of continual stepwise molt of primaries and bidirectional stepwise molt of the secondaries in these cormorants.

METHODS

I categorized specimens in first prebasic molt as subadults, and those that had molted all juvenal feathers as adults. Total numbers and nature of specimens examined for each season, age class, and geographic region are given in Table 1. Eighty-five (88%) of the 97 Blue-eyed Shag specimens examined were molting; 49 (72%) of the 68 King Shags were molting.

Primaries (excluding the remicle, P11) were numbered P1 to P10 from the carpal joint distally, and secondaries S1 to S15 (in two cases to S17) from the carpal joint to the humero-ulnar joint. Molt data were taken from all remiges when possible. Each remex was assigned to an age category 0–10 (1–5 are also growth categories): (0) juvenal; (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. This system reduces error due to the extended molt of cormorants, which results in remiges of varying ages that are not readily classifiable as "new" or "old" (pers. observ.); for this reason I did not use Ashmole's (1962) standard molt scoring system.

TABLE 1. Number of specimens of Blue-eyed and King shags examined for each season, age class, geographic region, and specimen nature.

	Blue-eyed Shag	King Shag
Season		
Winter (Jun–Aug)	4	9
Spring (Sep–Nov)	10	10
Summer (Dec–Feb)	60	39
Fall (Mar–May)	23	10
Age classes		
Juveniles	14	17
Subadults	33	20
Adults	50	31
Geographic region		
Southern South America	51	48
Falkland Islands	0	15
South Georgia Island	10	0
Shag Rocks (50°33′S, 42°02′W)	1	0
South Shetland Islands	17	0
Antarctic Peninsula	18	0
Macquarie Island	0	5
Specimen nature		
Museum skin	70	60
Freshly-killed	27	8
Totals	97	68

To determine whether the first prebasic molt (PB1) of primaries or of secondaries commenced first, and whether in the secondaries PB1 first commenced distally or proximally, I assumed that all secondaries and the primaries grow at approximately equal rates (as primaries apparently do in the Masked Booby, Dorward 1962; and in the Great Cormorant [*P. carbo*] and European Shag, Ginn and Melville 1983).

I considered molt of remiges symmetrical if feathers of each bilateral pair (L5, R5) were in the same age category or were molting simultaneously. Symmetry of remiges was expressed as the percent of individuals examined with completely symmetrical molt.

A "molt cycle" is the period from the beginning of one molt to the beginning of the next homologous molt (Humphrey and Parkes 1959). Because in stepwise molt homologous molts of remiges overlap temporally, I use the term "round" for the complete replacement of a feather row by one unidirectional wave (as in primaries), or by two waves that begin more or less simultaneously distally and proximally (as in secondaries); one round is thus the replacement of all feathers of a feather row (whether primaries or secondaries) by one molt cycle. A "molt wave front" is the most recently molted feather in a series of feathers of decreasing age (of a single wave of molt). The number of molt waves in remiges of each wing equals the number of wave fronts (P10 was considered a wave front when it was very new or molting).

RESULTS

Data on molt of remiges (coded in numerical age categories) for all individuals used in this study are available on request from the author.

PRIMARIES

In 24 cases in subadult Blue-eyed Shags (both wings in 10 birds, one wing in four birds), single-wave molt occurred in which the most distal nonjuvenal primary was the newest and the most proximal (P1) was the oldest; this occurred in 18 cases in subadult King Shags (both wings of nine birds). This shows that in subadults of both morphs PB1 (the first prebasic molt) commences at P1 and proceeds distally.

In subadult Blue-eyed Shags in which the second prebasic molt (PB2) had begun, PB2 started at P1 when PB1 had reached juvenal P5 ($n = 1$), P6 ($n = 1$), or P7 ($n = 1$). In seven Blue-eyed Shags, PB2 had not yet begun by the time P7 was replaced by PB1. In subadult King Shags in which PB2 had begun, PB2 started when juvenal P6 ($n = 1$) and P7 ($n = 1$) had been replaced by PB1. The beginning of PB2 marks the onset of stepwise molt, because from that point on PB1 and PB2 continue simultaneously (Fig. 1A).

In most cases, juvenal primaries were replaced sequentially, with P10 the last to be replaced. However, omissive molt (Cannell et al. 1983) occurred occasionally; in one Blue-eyed Shag, juvenal P8 and P9 were retained on both wings after P10 had been replaced, and in another juvenal P7 and P8 were retained on one wing and juvenal P7 on the other after more distal primaries had been replaced. In the King Shag, juvenal P6 was retained on both wings of one specimen, juvenal P7 on both wings of another, and juvenal P6 on one wing and P8 on the other wing of a third, all after more distal primaries had been replaced.

Adults of both morphs showed stepwise molt of primaries from proximal to distal (Fig. 1B). From zero to four waves occurred in primaries of each wing in adults of both morphs (Fig. 2). In 46 adult Blue-eyed Shags, $\bar{x} = 1.93 \pm 1.12$ waves per wing, and in 31 adult King Shags $\bar{x} = 2.39 \pm 0.88$ waves per wing.

Subadult Blue-eyed Shags had significantly more primaries molting per molting wave than did adults (Table 2). However, adults and subadults did not differ statistically in number of primaries molting per wing (Table 2).

Symmetry in molt of primaries between wings of individuals tended to be more common in subadults than it was in adults, although the differences were not statistically significant (Table 3).

SECONDARIES

PB1 of secondaries in both morphs began at the most distal and most proximal secondaries, and continued to the central secondaries (for an example, see Fig. 3A). In subadult Blue-eyed Shags in single-round (one-wave) molt of secondaries, two individuals had molt waves only in the distal secondaries (of both wings); four had molt waves only in the proximal secondaries (two in both wings; two in one wing). In those in single-round (two-wave) molt of secondaries, 10 had molt waves in both the distal and proximal secondaries. In single-round subadult King Shags, one individual was in single-wave molt of the distal secondaries (both wings); five were in two-wave molt, with waves in both the distal and proximal secondaries. In all of the waves, the wave front (centralmost) feather was either newer than or as new as any feather in the wave.

Of the six subadult Blue-eyed Shags in single-wave molt of secondaries, the highest number of feathers replaced by PB1 was five distal secondaries; in the only King Shag in this category, only two distal secondaries had been replaced.

Assuming that all secondaries grew at equal rates, in 11 Blue-eyed Shags in two-wave PB1 the distal wave started first in five individuals (both wings); the proximal wave first in both wings of two; and both waves simultaneously in both wings of two. In one specimen, the distal wave started first in one wing, the proximal in another; in another specimen the proximal wave started first in one wing and both waves started simultaneously in the other wing. In four King Shag specimens in two-wave PB1, the distal wave started first in both wings, the proximal started first in both wings of two others; and in one specimen the proximal started first in one wing, and both waves started simultaneously in the other wing.

In three cases in each morph, from one to four more peripheral juvenal secondaries (S1–S5, S10, S13) were retained after more central secondaries had already been replaced by PB1.

I interpreted data on relative ages of feathers as showing the beginning of PB2 in one Blue-eyed and one King shag specimen (for an example, see Fig. 3B). In the Blue-eyed Shag specimen, age categories (distal to proximal) of the secondaries were: (left wing) 2 1 8 8 2 0 0 0 0 0 0 0 0 0 2; (right wing) 7 2 8 8 1 0 0 0 0 1 8 8 8 8 1. In the King Shag specimen, the categories were: (left wing) 7 6 6 8 7 7 5 0 0 0 0 5 6 6 6.

In adult Blue-eyed and King shags which had apparently just resumed molt of secondaries after a pause (with at least 12 relatively new or older

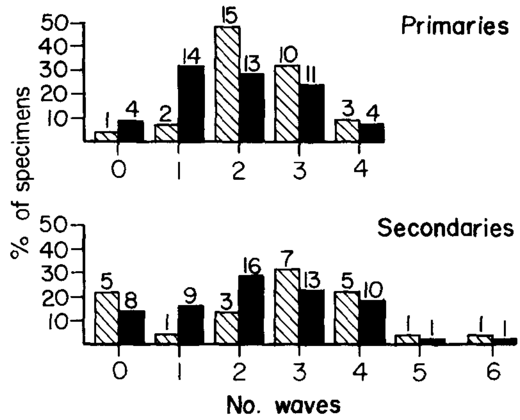

FIGURE 2. Number of waves in primaries and secondaries per wing in right wings of adult Blue-eyed and King shags. Left wings were used only if the right wing of that specimen could not be used. Cross-hatched bars represent King Shags; solid bars represent Blue-eyed Shags. Numbers above bars indicate n for each category.

secondaries per wing and no juvenal secondaries), each secondary occasionally appeared to molt first (of all the secondaries) after molt pauses (Fig. 4). The observation that any secondary was occasionally the first to be molted after molt pauses, and no secondary was overwhelmingly the most common to molt first, shows that in adults molt centers do not lie between S1 and S15.

In adult Blue-eyed Shags, there were nine cases in which a new wave had just begun at the most distal secondary, and two at the most proximal, while more central wave fronts (which apparently had distal points of origin) were molting. In adult King Shags, there were five cases of this in the most distal secondary and two in the most proximal. This shows that simultaneous waves occur in adults of both morphs, and that waves frequently start at S1 and S15.

TABLE 2. Comparisons between molts of remiges of adult and subadult Blue-eyed Shags.

	Subadults			Adults			
	$\bar{x} \pm$ SD	n	Range	$\bar{x} \pm$ SD	n	Range	P[a]
No. primaries molting/wave[b]	1.4 ± 0.7	63	1–3	1.1 ± 0.3	101	1–2	***
No. primaries molting/wing[c]	1.6 ± 0.7	63	1–3	1.9 ± 0.9	56	1–4	n.s.
No. secondaries molting/wave[b]	1.4 ± 0.6	37	1–3	1.1 ± 0.3	93	1–2	*
No. secondaries molting/wing[c]	2.2 ± 1.0	25	1–4	1.9 ± 1.1	49	1–6	n.s.

[a] Mann-Whitney U-tests between subadult and adult Blue-eyed Shags.
[b] For waves in which at least one feather was molting; n = number of waves examined.
[c] For feather rows in which at least one feather was molting; n = number of wings examined.
n.s. = $P > 0.05$, * = $P < 0.05$, *** $P < 0.001$.

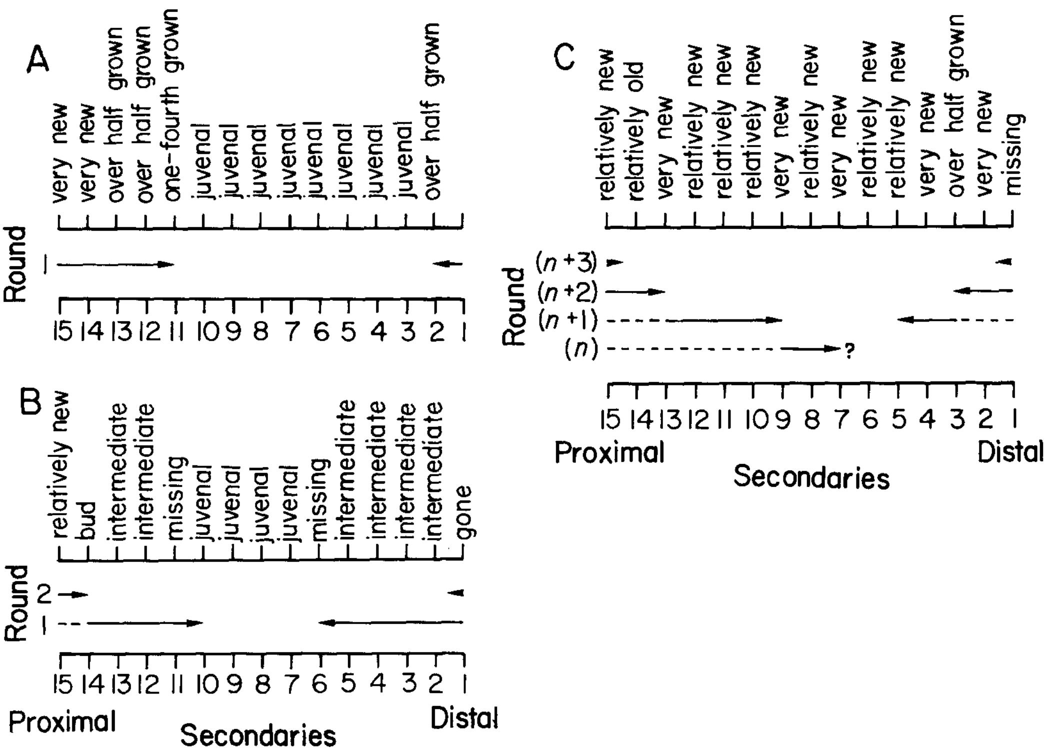

FIGURE 3. Stepwise molt of secondaries in Blue-eyed Shags. For explanation of conventions, see Figure 1. (A) subadult, KUMNH 81222, single-round molt. (B) subadult, KUMNH 81221; commencement of stepwise molt. (C) adult, AMNH (RHB 2714); multiple-round molt (exact number of rounds and direction of centralmost wave cannot be determined).

Adults of both morphs had from one to six waves per wing in secondaries (Figs. 2, 3C; mean number of waves in right wings of Blue-eyed Shags was 2.26 ± 1.42 [n = 50]; mean number in King Shags was 2.56 ± 1.73 [n = 23]).

Subadult Blue-eyed Shags had significantly more molting feathers per wave in secondaries than did adults (Table 2). However, numbers of secondaries molting per wing did not differ between subadult and adult Blue-eyed Shags (Table 2); this implies that subadults had marginally fewer waves per wing than adults.

Symmetry between wings of each specimen appeared more common in molt of secondaries in subadult Blue-eyed and King shags than in adults, but the differences were not statistically significant (Table 3). Although symmetry appeared less common in molt of secondaries than in primaries for each age class and morph, none of the differences were statistically significant (Table 3).

MOLT DURING NESTING

Five adult Blue-eyed Shags collected while nesting were molting from 0–4 ($\bar{x}$ = 2.2 ± 2.5) pri-

TABLE 3. Percent (n) of Blue-eyed and King shags with complete symmetry in molt of remiges.

	Blue-eyed Shag			King Shag		
	Subadults	Adults	P[a]	Subadults	Adults	P[a]
Primaries	13 (20)	6 (38)	2.9 n.s.	4 (9)	2 (17)	0.6 n.s.
Secondaries	6 (15)	3 (38)	0.9 n.s.	2 (9)	0 (12)	0.2 n.s.
P[a]	0.5 n.s.	0.1 n.s.		0.2 n.s.	0.1 n.s.	

[a] χ^2 tests, df = 1; n.s. = $P > 0.05$.

maries and from 0–3 ($\bar{x} = 1.4 \pm 1.5$) secondaries. One adult King Shag was molting two primaries and another was molting two secondaries while nesting. One subadult King Shag was molting one primary and three secondaries while nesting.

DISCUSSION

PRIMARIES

Stepwise molt of primaries of Blue-eyed and King shags is similar to that of the European Shag (Potts 1971). The second prebasic molt begins when the first has replaced P8 in the European Shag (*n* not given, Potts 1971), the Great Frigatebird (*Fregata minor, n* = 3, DeKorte and DeVries 1978), the Brown Booby (*Sula leucogaster, n* = 1, Dorward 1962), or P7 in the Masked Booby (*n* not given, Dorward 1962). The Blue-eyed Shag is the only continual stepwise-molting species yet studied for which variation is known in timing of the beginning of PB2 in primaries in relation to progress of PB1, but it probably varies in other species as well. Blue-eyed and King shags occasionally have more molt waves in primaries than occur in the the Great Cormorant, the Bank Cormorant (*P. neglectus*), and the Rock Shag (the latter three have one to two waves, three rarely; Ginn and Melville 1983, Cooper 1985, Rasmussen 1987). The Red-legged Shag (*P. gaimardi*; unpubl. data) and the European Shag (Potts 1971) also have four molt waves in the primaries.

Data from Blue-eyed and King shags confirm Stresemann and Stresemann's (1966) assertion that continual, not periodic, stepwise molt occurs in cormorants. I did not find specimens with growth sequences in primaries in which a more proximal, new wave front was about to overgrow an older, more distal wave front, as would be predicted for periodic stepwise molt. Also, age discontinuities frequently occurred within waves (due to molt pauses) in both morphs; these would not occur in periodic stepwise molt.

Murphy (1936) was incorrect in stating that the new primaries of the King Shag do not reach maximum length until July or August; in this morph, as in the Blue-eyed Shag, primaries reach maximal length during all seasons of the year. Bernstein and Maxson (1981) noted that an Antarctic Blue-eyed Shag had some old remiges in July, "probably indicating that a complete moult had not occurred in June." This may be explained by the fact that, although pauses occur,

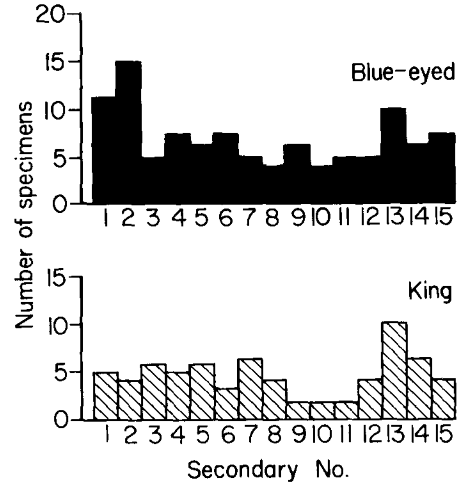

FIGURE 4. Frequencies in which each secondary is very new or molting (in adults in which at least 12 secondaries per wing are relatively new or older).

stepwise molt of the remiges in adult cormorants cannot be considered completed at any time, since new waves begin before completion of the previous waves.

SECONDARIES

Although Ashmole (1968) suspected that the Fairy Tern (*Gygis alba*) has stepwise molt of secondaries, this has been confirmed only for the Rock Shag (Rasmussen 1987), and bidirectional stepwise molt has not been described. On the basis of the following evidence from the molts of Blue-eyed and King shags, I extend the definition of stepwise molt to include "bidirectional stepwise molt of secondaries:" (1) molt centers (points from which molt waves regularly begin) occur only at S1 and S15, and thus molt must be bidirectional; (2) up to six simultaneous waves occur within secondaries of one wing (a new wave often had just begun in the most proximal or most distal secondary, while growth was occurring at more central wave fronts which had distal points of origin; in the absence of central molt centers, this demonstrates the occurrence of stepwise molt); (3) the ontogeny of molt of secondaries is similar to that of stepwise molt of primaries, in that the second round begins before completion of the first round, thus initiating two-round molt (the first prebasic molt of secondaries consists of one round of two waves, instead of one wave as in the primaries).

CONSEQUENCES OF STEPWISE MOLT

In the Fairy Tern (a continual stepwise-molting species) each primary is apparently replaced every year, each molt wave pauses for the season at the point where the next more distal wave began that season, and molt waves continue where they leave off (Ashmole 1968). It is thought that there are more waves per wing in older individuals of stepwise-molting species (DeKorte and DeVries 1978), as Dorward (1962) found for the Masked Booby. However, the number of waves must stay the same if every feather is replaced exactly once per year and all waves start at P1. This is the case in the European Shag, in which not all primaries are replaced each year (Potts 1971), and the occasional occurrence of very old primaries in adult Blue-eyed and King shags shows that they also do not replace all primaries yearly. The ontogeny of stepwise molt in the Fairy Tern is not known, but it must differ from that of these cormorants if the molt features listed above are invariant in this tern.

Berry (1976) stated that a disadvantage of stepwise molt in cormorants is that outer primaries are retained longer, but failed to note that this disadvantage is restricted to subadults. However, in adult cormorants wing tip primaries are usually replaced each year by a different round, so at any time there are few or no very worn primaries, and these are not restricted to the wing tip.

Potts (1971) asserted that the disadvantage of subadults retaining worn outer primaries is presumably outweighed by the advantages of their having a slow molt that is energetically relatively nondemanding. However, because most species of cormorant molt to some extent during breeding and winter (Turbott 1956, Dorward 1962, Stonehouse 1962, Nelson 1964, Potts 1971, Berry 1976, DeKorte and DeVries 1978, Bernstein and Maxson 1981), stepwise molt appears to be advantageous in adults as well in that it allows slow molt throughout the year. Stepwise molt of remiges in cormorants and other pelecaniforms may also have the adaptive advantage of allowing full flight capabilities year-round with minimal disruption. In stepwise molt of adults smaller gaps of molting feathers occur at more sites in the wings, rather than larger gaps at fewer sites (Table 2) as occur in subadults.

Subadult Blue-eyed Shags have marginally more molting feathers per wave than do adults but do not differ from them in number of molting feathers per wing; this implies that subadults have fewer waves per wing than do adults (Table 2). Subadults also commence molt with a single wave of descendent molt. Therefore their molt is more similar to that of nonstepwise molting birds, including the Procellariiformes, which have single-wave descendent molt from P1 to P10 (Stresemann and Stresemann 1966, Hunter 1984). Single-wave descendent molt of primaries is thought to be the primitive mode of molt of primaries in birds (Stresemann and Stresemann 1966), and Procellariiformes are often considered the most appropriate outgroup to the Pelecaniformes (Cracraft 1985). This and the ontogeny of primary molt in shags shows that continual stepwise molt in the Pelecaniformes is derived. Since all pelecaniforms in which molt has been studied show continual stepwise molt of primaries, this type of molt is a synapomorphy (shared derived character) for this order. Early Pelecaniformes are known from the Eocene of Wyoming and Britain (Harrison and Walker 1977, Olson 1977), and tropical conditions such as existed at that time (Martin 1983) seem to favor stepwise molt, because several Recent tropical groups (e.g., some tropical Tinamiformes, Galliformes, and Columbiformes; *Opisthocomus*, and *Colius*; Stresemann and Stresemann 1966) have evolved it independently. The Pelecaniformes are the only group with Recent nontropical representatives that have continual stepwise molt. Stepwise molt thus likely evolved in a pelecaniform ancestor during the early tropical period of their history, and as far as known has been retained by all descendent species.

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