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UNUSUAL PATTERNS OF INCOMPLETE PRIMARY MOLT IN LAYSAN AND BLACK-FOOTED ALBATROSSES[1]

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Abstract. Laysan and Black-footed Albatrosses show a bidirectional pattern of incomplete molt in their primaries which has never before been described for any bird. Juveniles molting their flight feathers for the first time replace only their distal three or four primaries. In older birds the ten primaries are divided at their mid-point into two series, each with an independent set of rules for replacement. Unlike most other birds, the primaries of the two series are replaced in opposite directions, with molt proceeding toward the wing tip in the outer series and toward the body in the inner series. The outermost feathers of the distal series are replaced every year without fail; the time available to molt determines how many feathers of this series are replaced. In the inner series, feather replacement occurs only every second to third year. When molt does occur in the inner series it is normally incomplete, and it proceeds in a wraparound pattern which assures that the oldest and most worn feathers are always the first to be replaced.

Key words: Diomedea immutablis; Diomedea nigripes; *albatross; wraparound molt; stepwise molt; incomplete primary molt; bidirectional primary molt.*

INTRODUCTION

Laysan Albatrosses (*Diomedea immutablis*) and Black-footed Albatrosses (*Diomedea nigripes*) show a unique pattern of bidirectional incomplete molt in their primaries. In this paper, we describe the primary molt, analyze differences in molt patterns between age and sex classes, and show that there is significant individual variation in the replacement of primaries. This is the first of a series of papers that interprets patterns of incomplete primary molt in the context of condition, time constraints, and life history tradeoffs. In a second paper, we show that differences between Laysan Albatrosses in their patterns of molt correlate with parasite levels, suggesting that variation in individual condition plays a role in shaping molt variation. In a final paper, we show that primary molts in Laysan and Black-footed Albatrosses are constrained by time limitations, and we argue that patterns of molt should be

interpreted in the context of life history tradeoffs between current and future reproduction.

Molt is energetically demanding and time consuming for birds, whatever their size or molt strategy (Murphy and King 1991). During the molt, feather synthesis increases energetic demands, and gaps created by growing feathers reduce flight performance, making foraging more costly. For example, flight feather molt is known to increase the difficulty kestrels have foraging (Masman et al. 1988) and to render albatrosses more vulnerable to mortality during storms (Kinsky 1968). Most birds do not replace flight feathers and breed at the same time (Payne 1972, King 1981, Walsberg 1983). For large birds such as albatrosses with long primaries, the time it takes primaries to grow makes molt particularly problematic, since there may not be time in a single year to breed and replace all primaries. Therefore, many large birds have evolved particularly complex strategies to meet the demands of feather replacement.

The more feathers that a bird replaces at once, the faster it completes the molt, but the more aerodynamic efficiency is reduced. In the most

extreme case, many water birds simultaneously replace all of their flight feathers and lose the ability to fly during their molt. An alternate strategy common to large seabirds is incomplete molt, in which replacement of the primaries is interrupted by breeding (e.g., Stresemann and Stresemann 1966, Potts 1971, Rasmussen 1988). Incomplete molts are compromises which allow for a shorter molt and slightly reduced flight efficiency. However, since all the primaries aren't replaced each year, worn feathers accumulate in the wing. This can have important reproductive consequences. A succession of incomplete molts may result in the generation of so many over-worn flight feathers that birds must skip breeding to be able to replace all their worn primaries.

There are several possible patterns of feather replacement for birds that undergo incomplete molts. Ornithologists have tended to interpret the presence of different aged feathers within a single wing as evidence of one particular pattern, **stepwise molt** (Brooke 1981, Cooper 1985, Furness 1988, Harris 1973, Stresemann and Stresemann 1966). Because we had noted a variety of feather ages in the wings of Laysan and Black-footed Albatrosses, we began this study to test the set of stepwise molt rules that hold for other large birds with incomplete molt, specifically Black-crowned Night-herons *Nycticorax nycticorax* (Shugart and Rohwer, unpubl. manuscript) and various Shags (Potts 1971, Rasmussen 1988). Yet as we show below, albatrosses violate the rules of stepwise molt, and instead replace their primaries in a pattern we term **wraparound molt**. In this paper, we describe four possible patterns of incomplete molt, and we develop a series of tests to determine which pattern a given species follows. We argue that these distinctions between molt patterns are important, since different types of incomplete molts generate different accumulations of old and worn feathers, which can have future reproductive consequences.

METHODS

NATURAL HISTORY

Laysan and Black-footed Albatrosses breed in shared colonies in the North Pacific, largely on the leeward Hawaiian Islands (Rice and Kenyon 1962a). Like all other albatrosses, Laysan and Black-footed Albatrosses have single egg clutches and extremely long breeding seasons. Black-footed Albatrosses begin arriving at their breeding

colonies in late October; their mean lay date is November 21, and they incubate eggs for about 65 days. The mean hatching date for Black-footed Albatrosses is 25 January, and the nestling stage lasts for approximately 140 days. Black-footed Albatrosses depart the breeding colonies in mid-June, and head for the North Pacific where they molt (Rice and Kenyon 1962b). Laysan Albatrosses arrive at the breeding colonies in early November, about two weeks later than Black-footed Albatrosses. The mean lay date for Laysan Albatrosses is November 30. They incubate for about 64 days; the mean hatch date is February 2; and the nestling stage lasts approximately 165 days, 25 days longer than for the Black-footed Albatrosses. Laysan Albatrosses depart from the breeding colonies in mid-July, and head for the North Pacific to forage and molt (Rice and Kenyon 1962b).

Six years of age seems to be the earliest that both Laysan and Black-footed Albatrosses nest (Rice and Kenyon 1962b). More often, it appears, birds do not attempt to breed until they are nine years old (Fisher 1976). Subadults from the ages of three years on return to the breeding colony at about the same time adults return to breed. These subadults court, mate, and often build nests (Rice and Kenyon 1962b).

Both Laysan and Black-footed Albatrosses weigh about 2.5 kg (data from this sample), which makes them among the smallest of the albatrosses. Males and females are the same size. Males incubate for longer periods than do the females, and feed young as much as females (Rice and Kenyon 1962b). Both species show strong affinity to established nest sites and mates. If a bird looses its mate, it takes at least two years to re-mate and successfully breed again (Rice and Kenyon 1962b, Fisher 1976). Successful breeders are more likely to skip breeding the next year than unsuccessful breeders. Eighty-seven percent of birds that failed in their breeding returned the following year, but only 66% of successful birds return. Annual adult mortality is between 6 and 8% (Rice and Kenyon 1962b, Fisher 1976). Thus, among adults that successfully fledge young, about 25% will survive but skip breeding the following year (Rice and Kenyon 1962b). Fisher (1976) found similar percentages of adults that failed to breed. In one year, out of 617 adults that attempted breeding, 75% returned to breed the next year. Eighty percent of failed breeders returned, and 68% of successful breeders returned, per-

centages which closely agree with Rice and Kenyon's figures (1962b).

Neither Laysan and Black-footed Albatrosses nor other albatrosses molt during the breeding season. Therefore, the extended length of their breeding seasons leaves them relatively little time to molt for their size. They are away from the breeding colonies for four months each year, leaving them at the most about 110 to 120 days to molt, depending on when they finished breeding. Since Laysan Albatrosses spend, on average, about two weeks longer at the breeding colony, they have less time available to molt.

THE DRIFT-NET OBSERVER PROGRAM

Nonbreeding Laysan and Black-footed Albatrosses have been largely inaccessible to ornithologists because they winter in the middle of the North Pacific (from 28°00′ to 45°00′N and 150°00′ to 175°00′W, data from this sample). In 1990 from May to November, and in 1991 from February to November, 191 Laysan and 117 Black-footed Albatrosses were recovered as by-catches from squid drift-nets, as part of an international investigation of the impact of the squid fishery on non-target species (see Johnson et al. 1992 for details of the salvage operation and mortality data). Ninety-one percent of these albatrosses were caught in the nets from June to October, during the period of active molt. Carcasses were frozen when the birds were removed from the squid nets, usually within twelve hours of drowning. The birds were shipped to the University of Washington Burke Museum in Seattle, Washington, where they were prepared as pelted skin/extended wing/skeleton/tissue combination specimens. Preparators measured the length and width of bursas at the time of preparation, to aid in aging the specimens (Broughton 1994).

SCORING MOLT

Growing feathers. We scored wing molt as follows. We gave growing primaries and secondaries a decimal fraction (scored as 0.1 to 0.9) to indicate what fraction of their length had been attained. In 26 specimens where the relative length of adjacent feathers had to be assessed precisely to be confident about the direction of molt, we also measured the length of the growing feathers with a 380 mm metal rule to 1 mm. On seven Laysan and seven Black-footed Albatrosses, we measured the length of fully grown feathers. Fully grown feathers that appeared to have

been newly replaced were examined at their bases for evidence of sheathing. Feathers that were essentially fully grown but that had sheathing at their bases were assigned growth scores of 0.9 to indicate their recent replacement.

Fully grown feathers. We aged full length flight feathers by two characters: color and wear. Aging fully grown feathers was a difficult task, because within a wing, the inner primaries and secondaries receive much less wear than the outer most primaries. Between wings, however, there is also substantial variation in the appearance of feathers replaced in a given year, because of seasonal variation in collection dates, and probably also because of behavioral differences between birds. Therefore, we had to develop a method of aging feathers that recognized both variation within a wing, as well as variation between birds.

There are two general ways to age feathers. One way, that has the virtue of objectivity, is to focus on *variation between wings*. First, one establishes a set of comparison specimens with feathers that show different degrees of color and wear, and then one independently assigns a wear and color score based on those comparison specimens. Uniform wear-class scores are then assigned to all specimens, regardless of date of collection. Then for each primary, the scores for all the birds are pooled to derive estimates of the age classes. By waiting to assign age class scores, this means that feathers are categorized between wings rather than within wings, and all within-wing comparisons are lost. Seasonal or behavioral variation between birds will confound the results from this method.

We used an alternate method, which focuses on *within-wing* variation in color and wear, and so assigns age scores based primarily on comparisons to other feathers within the wing. In this method, growing feathers and newly grown feathers (with sheathing at their bases) are unambiguously new, and so assigned an age score of 0. In our albatrosses, older feathers fell into one, two, or three additional color and wear classes, which we considered to be feathers replaced one, two, or three years earlier. Feather colors fell into four classes, which we used to age feathers without sheathing. Growing feathers and feathers that we knew had just been replaced (due to sheathing at their base) were nearly black, feathers that had been molted the preceding season were a dark brown, feathers that had not been replaced for two years were light brown,

and feathers that were three years old were an even lighter brown. Three-year-old feathers were rare, while two-year-old feathers were common. Among the inner primaries, the most obvious difference between new and year-old feathers was in color, whereas two and three year old feathers showed substantial and obvious wear. However, comparisons of unambiguous year-old and new feathers under a 2× magnifying light showed consistent fraying on the barb tips of year-old feathers. We used this fraying to help age feathers in wings where there were only subtle color differences between newly replaced and feathers a year older.

Feathers judged to have been replaced not in the current molt but in the previous molt a year earlier were given an age = 1; feathers judged to be a year older were classified age = 2, and feathers one year older were classified age = 3. Many molting specimens had feathers of three age classes (Table 6).

We also assigned primaries "wear scores" based on how worn those feathers appeared relative to other primaries with the same age score. The purpose of these decimal fractions was to preserve records of subtle differences between feathers and, at the same time, to record which year class we thought an ambiguous feather should be assigned to. A score of 1.6–1.9 indicates feathers we treated as two-year-old feathers that were less worn than normal, while a score of 2.1–2.4 indicated feathers we treated as two-year-old feathers that were more worn than normal. Scores of 0.5, 1.5 and 2.5 were not allowed, thus forcing us to assign feathers to our best estimation of their year class.

This special scoring system accomplished three things. It preserved our best estimate of year classes based on comparisons with the molting birds. It did not hide ambiguous specimens. Finally, it forced us to make decisions about the best assignment of feathers to age classes while the wings were being examined, rather than through an arbitrary pooling of a uniform set of wear-class scores assigned to all specimens, regardless of date of collection. Feathers within each wing were extensively compared with other feathers within the same wing, as well as with feathers from other wings collected during the same time of season, but we did not allow ourselves to merely assign wear and color scores to each feather which later would have to be converted to year classes. Because birds show sub-

stantial differences in the average state of their primaries, due both to when in the year they were collected, and probably to behavioral differences, we believe that comparisons that focus only on differences between birds would be less reliable.

Although comparisons within wings do take account of variations between birds, they too can lead to substantial problems, because albatross feathers receive very different amounts of wear depending on their position in the wing. The inner primaries receive relatively little abrasion, while the outermost primaries are subject to severe abrasion from water and sand because, as we later learned, Laysan and Black-footed Albatrosses sometimes drag the tips of their wings in the water and also on the sand while soaring (Jeffrey Marks, pers. comm.).

When we assigned age scores, we noted that outermost primaries appeared much older than inner primaries, based on within-wing scores. In actively molting birds, the outer primaries (usually p9 and p10) that had not yet been molted were so worn that they were always scored as two-year-old feathers (wear score 1.6 to 2.4) based on within-wing comparisons, since the feathers appeared to be too old to have been replaced the previous year and were more worn than any inner primaries which had not been replaced. However, when we finished scoring all the molting and nonmolting birds, we realized that out of 96 specimens that had finished or nearly finished their molt, we did not have a single specimen that had stopped molting with an outer primary greater than age class = 0. This implied that each year, all birds replaced their outermost primaries, and furthermore it meant we had overestimated the age of the outer two primaries. To obtain numerous birds with outer primaries of age = 2 at the beginning of one molt, there would need to have been birds at the completion of the previous molt with outer primaries that hadn't just been replaced, scoring age = 1. Therefore, in actively molting birds and in birds that had just finished breeding and were about to begin their molt, we treated any of primaries 8 to 10 as age class = 1 if they had been scored as age class = 2.

Nonmolting birds. Birds that had just finished their molt were scored in the same way as birds in active molt: recently replaced feathers were given a score = 0, and so on. Birds captured from February to June, that had not yet begun their molt, were scored so that feathers replaced in the
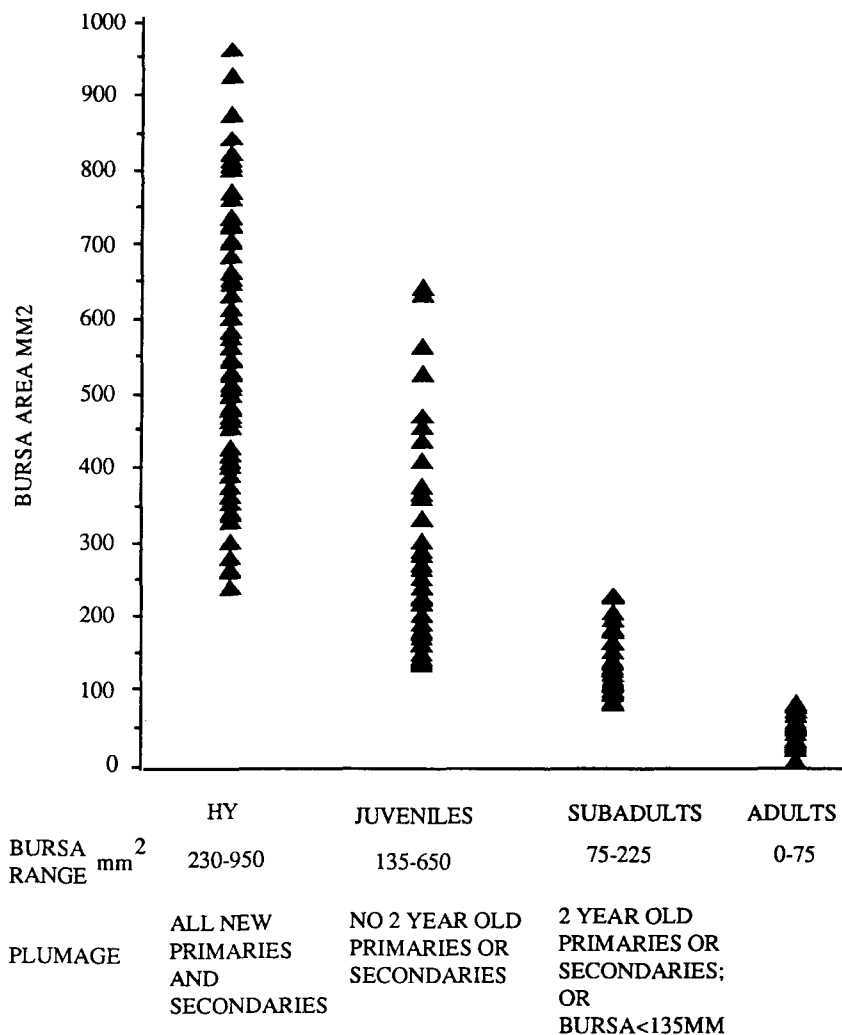
FIGURE 1.   The range of bursa areas and plumage criteria for each age class of Laysan and Black-footed Albatrosses.

last molt, nearly a year before, were aged = 1, and so on. When these birds (actively molting, finished molting, and pre-molting) were combined in several analyses, the feather age classes were standardized, so all feathers replaced in the most recent molt were scored = **new,** all replaced in the previous molt were scored = **previous molt,** and so on.

In our analyses of the molt patterns for both juveniles and older birds, we included some birds that had finished and others that had nearly finished their molt. We defined birds as nearly finished molting if they had begun growing p10,

since as we show below, all birds replace p9, and p10 was the last feather to be replaced in all birds. We could therefore include birds that were nearly finished molting and still be confident that we were counting all the primaries that they were likely to molt in that molt cycle. If we had excluded these birds, our samples sizes would have been very low, since we had few birds that had completely finished the molt. Because only one extended wing per specimen was prepared, we could examine flight feather molt on only one wing, so we do not have any information about symmetry in molt patterns.

TABLE 1. The distribution of age classes and sex ratios in the drift-net sample of Laysan and Black-footed Albatrosses.

Age class	Age	Laysan					Black-footed				
		n	%	% Males	% Females	Mean bursa area mm^2	n	%	% Males	% Females	Mean bursa area mm^2
HY	4–10 months	66	35	50	50	556	31	26	48	52	646
Juveniles	16–22 months	37	19	49	51	217	34	29	35	65	349
Subadults	34 months–6 years	34	18	56	54	132	16	14	44	56	126
Adults	≥6 years	54	28	20	80	27	36	31	31	69	20

ASSIGNING BIRDS TO AGE CLASSES

We separated the albatrosses into four age classes, using a combination of molt and bursa area. The bursa of Fabricus is a blind diverticulation off the gut near the cloaca that serves the immune system in young birds. Bursas are large and fleshy in pre-breeders, but atrophy when the sex steroids become active, and in these two species of albatrosses, bursa size is inversely correlated with gonad size (Broughton 1994). In Laysan and Black-footed Albatrosses, a series of known-age banded birds showed that bursa involution is advanced by the third year of the bird's life (Broughton 1994), which is when subadults begin showing up at breeding colonies, even though they rarely breed before they are seven years of age (Rice and Kenyon 1962b, Fisher 1976). Because birds resorb their bursas at different rates (Broughton 1994), we used a combination of feather age and bursa size to age the birds. Figure 1 shows the range of bursa sizes (length × width) in each age class, and the additional plumage criteria we used to age these birds. We checked these plumage and bursa criteria against known-age banded birds in our sample.

Albatrosses were classified as **hatch year** if all ten primaries and all thirty-odd secondaries were new. These were birds from four to ten months old that had not yet undergone their first flight feather molt. Since hatch year birds have all new juvenile feathers, they tell us little about incomplete molt patterns, and we exclude them from the analysis. **Juveniles** were birds with bursas

TABLE 2. The percent of juveniles that began their first primary molt at each feather.

	Primary number			
	p6	p7	p8	p9
% Laysan, $n = 34$	10	26	59	6
% Black-footed, $n = 30$	0	22	73	3

greater than 135 mm^2 that had no feathers older than one year. In our sample they are from 16 to 21 months old, were born during the previous breeding season, and if molting, are undergoing their first molt of flight feathers. **Subadults** are birds with bursas greater than 75 mm^2; if bursas were greater than 135 mm^2, they had some two-year-old primaries. Subadults were born at least two breeding seasons earlier, but are not yet at breeding age, so they are between 22 months and six years old. **Adults** are birds with bursas less than 75 mm^2, and therefore likely to be of breeding age, from six years on. Some younger birds may be included in this age class, if they resorbed their bursas entirely before beginning breeding. Substantial numbers of adults had all new primaries, but none had all new primaries and all new secondaries.

Table 1 shows the distribution of age classes in our sample, which differs from distributions observed at breeding colonies (Fisher 1976, Rice and Kenyon 1962b); there are more hatch year and young birds in our sample. This may be caused by a higher representation of young birds foraging at drift nets, and/or by their greater likelihood of entanglement due to inexperience.

To help in following the results, we include a diagram showing primaries and secondaries and the direction of feather replacement (Fig. 2). Primaries are numbered from the wrist outwards, from 1 to 10. In this paper, primaries 6–10 are called the distal or outer series; primaries 1–5 are called the proximal or inner series.

RESULTS

MOLT OF JUVENILES

Juvenile Laysan and Black-footed Albatrosses replace only their distal three or four primaries (typically p8, p9, and p10) and do not molt their inner primaries until at least the following year. Figure 3 shows the distribution of new and old
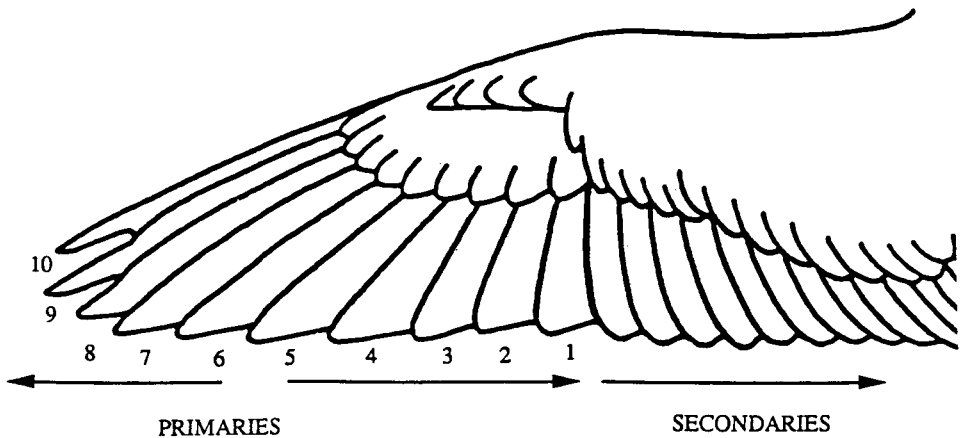
FIGURE 2.   The primaries and secondaries of a bird (modified from Edelstram 1984). Laysan and Black-footed Albatrosses have 10 primaries and 30 secondaries (not all are shown). Numbers indicate primary numbers; lines indicate direction of molt but not necessarily nodes of molt series, which vary as explained in the text.

primaries in juveniles that had finished (or nearly finished) molting. All the juveniles molted at least two of their outer three primaries, and none of the juveniles molted any of their inner primaries (p1 to p5). The number of primaries molted by juveniles does not differ between species (means throughout the paper are reported ± SE; Laysan Albatrosses $n = 34$, $\bar{x} = 3.6 \pm 0.2$; Black-footed Albatrosses $n = 30$, $\bar{x} = 3.3 \pm 0.1$, Mann Whitney test, $Z = -0.319$, $P = 0.7$).

Juveniles molt their outer primaries in sequence from proximal to distal. The location of the molt node—defined as the feather that begins the molt—is shown in Table 2. Most juveniles start with p8 (59% of Laysans and 73% of Blackfoots), but a few start with p7, p6 or p9. The location of molt nodes does not differ between the two species ($\chi^2 = 1.14$, df = 3, $P = 0.8$). No matter which feather juveniles start with, they always molt outward. Moreover, they always complete the outer primary molt: for example, if they start with p7, they always molt p7, p8, p9, and p10. Only one juvenile out of 64 skipped a feather in the molt sequence.

Older birds replace more primaries than juveniles in both species (Table 3). We reasoned that if juveniles are molting fewer primaries than adults because of energetic constraints due to poorer foraging ability, then they should be molting fewer secondaries as well. Alternatively, juveniles might make a molt effort equal to that of adults, but trading off secondary replacement for primary replacement, in which case we would see juveniles molting more secondaries than adults do. We found our first hypothesis supported: juvenile Laysans molt significantly fewer secondaries as well as fewer primaries than adults, and juvenile Black-footed Albatrosses tend to molt fewer secondaries than adults, although the difference is not significant (Table 3).

ADULT PATTERNS

For both Laysan and Black-footed Albatrosses, the differences in molt patterns between sexes or between subadults versus adult birds are not statistically significant (Table 4). However the species do significantly differ in their molt patterns: Black-footed Albatrosses replace more primaries than Laysan Albatrosses (Laysan $n = 89$, $\bar{x} = 5.7 \pm 0.4$ primaries; Black-footed $n = 52$, $\bar{x} = 7.1 \pm 0.5$ primaries, Mann Whitney $Z = -2.0$, $P = 0.04$). Therefore, we examined the two species separately, but combined the two sexes and the two older age classes in the following analyses. Subadults (between two and six years, prebreeders) and adults (those without a bursa, seven years or older) are together referred to as older birds.

Figure 4 shows the distribution of new primaries in older Laysan and Black-footed Albatrosses. As with juveniles, nearly all older birds replace their outer three primaries each year: 97% of the Laysan and 94% of the Black-footed Albatrosses replaced p8, 9, and 10. Table 5 shows that primaries of the inner series are often retained for two years and, in some birds, a few of these feathers may be three or four years old.

TABLE 3. Number of primaries and secondaries replaced by juveniles versus older birds. Includes birds finished molting or nearly finished molting. P-values from Mann-Whitney tests.

	Laysans				Black-footed			
	Juveniles	Older birds	Z	P	Juveniles	Older birds	Z	P
Number of primaries replaced, $\bar{x} \pm$ SE	3.6 ± 0.2 $n = 34$	5.7 ± 0.3 $n = 62$	−3.3	0.0009	3.3 ± 0.1 $n = 30$	7.2 ± 0.5 $n = 37$	−3.9	0.0001
Number of secondaries replaced, $\bar{x} \pm$ SE	6.8 ± 0.2 $n = 34$	10.6 ± 0.7 $n = 62$	−4.1	0.0001	10.1 ± 0.2 $n = 30$	12.2 ± 1 $n = 37$	−1.2	0.08

TABLE 4. Differences between sexes and age classes in the number of primaries and secondaries replaced.

|	Males	Females	Mann Whitney U test		Subadults	Adults	Mann Whitney U test		Total
			Z	P			Z	P	
Laysan									
Number of primaries replaced, $\bar{x} \pm$ SE	6.6 ± 0.6 $n = 23$	5.2 ± 0.4 $n = 39$	−2	0.04	5.9 ± 0.6 $n = 22$	5.6 ± 0.6 $n = 40$	−0.18	0.9	5.7 ± 0.3
Number of secondaries replaced, $\bar{x} \pm$ SE	12.2 ± 1.3	9.7 ± 0.8	−1.6	0.12	12.4 ± 1.4	9.7 ± 0.8	−1.5	0.12	10.6 ± 0.7
Black-footed									
Number of primaries replaced, $\bar{x} \pm$ SE	7.1 ± 0.8 $n = 14$	7.3 ± 0.6 $n = 23$	−0.3	0.7	5.9 ± 1.2 $n = 8$	7.6 ± 0.5 $n = 29$	−1.3	0.2	7.2 ± 0.2
Number of secondaries replaced, $\bar{x} \pm$ SE	13.1 ± 1.8	11.7 ± 1.3	−0.6	0.6	8.9 ± 2.2	13.1 ± 1.1	−1.8	0.07	12.2 ± 1.0
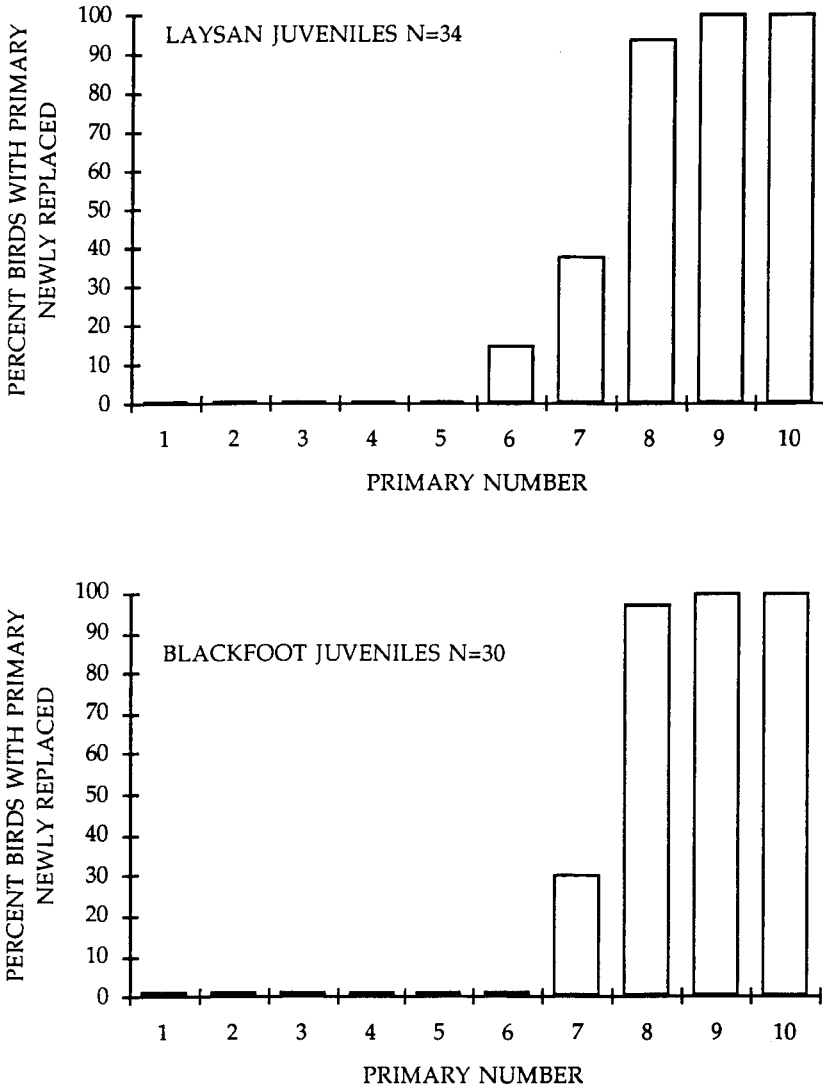
FIGURE 3. Molt in juveniles: the probability of a feather having been replaced versus its position in the primary sequence. Includes birds finished molting or nearly finished molting.

BIDIRECTIONAL MOLT SERIES

We define a molt series as an adjacent set of flight feathers that are molted according to a single set of rules (the "moult unit" of Edelstam 1984). The primaries of adult Laysan and Black-footed Albatrosses are organized into two molt series: an outer series, which is replaced in sequence from p6 to p10, and an inner series which is replaced in the opposite direction, in sequence from p5 to p1. Evidence for bidirectional molt comes from the length of actively growing feath-

ers. Table 6 shows the molt scores for each primary of all older birds with actively growing inner primaries (p5–p1). An examination of this table shows that molt typically proceeds from proximal to distal for primaries 6 to 10; while from p5 to p1, molt proceeds from distal to proximal. For example, look at id = 17. Primary 5 has grown to 91% of its total length, while p4 has grown to only 86% of its total length, and p3 to 30% of its length, while p2 has not yet been replaced. What this means is that of these feathers, p5 was the first one replaced, then p4, then

TABLE 5. Distribution of new and old primaries in older birds (subadults and adults combined). Includes birds finished or nearly finished molting. Primary ages: 0 = replaced in most recent molt, 1 = not replaced in recent molt but replaced in the previous molt, 2 = replaced in molt two years before.

| | | | | | Number of birds with primaries of a given age | | | | | |
| | | | | | Primary number | | | | | |
Primary ages	p1*	p2	p3	p4	p5	p6	p7	p8	p9	p10*
					Laysan					
0	26	22	17	21	23	24	38	60	60	60
1	35	36	41	41	36	34	19	2	2	2
2	0	4	4	0	3	4	4	0	0	0
3	0	0	0	0	0	0	0	0	0	0
					Black-footed					
0	23	22	19	17	21	26	28	35	35	34
1	14	14	16	18	16	10	7	2	2	2
2	0	0	1	1	0	1	2	0	0	0
3	0	1	1	1	0	0	0	0	0	0

* Counts for Laysan Albatrosses for p1 total less than 62 because one bird was missing p1. Likewise, counts for Black-footed Albatrosses for p10 total less than 37 because one bird was missing p10.

p3. In contrast, a look at p6, p7, and p8 shows that the outer series proceeded in the opposite direction: p6 was replaced first, then p7, then p8, while p9 and p10 had yet to be replaced.

Support for the claim that molt proceeds in two different directions within the wing, and that the break between molt series occurs in the middle primaries, is summarized in Table 7. For each older bird in active molt, each growing primary was scored one of four ways.

(1) If the growing focal feather showed that molt was unambiguously proceeding outwards, from proximal to distal, the feather was scored "+." This occurred when the focal feather either was less advanced in its growth than the next proximal feather, or when the focal feather was more advanced in its growth than the next distal feather (but not more advanced in its growth than the next proximal feather, if that feather was growing).

(2) If the growing focal feather showed that molt was unambiguously proceeding from distal to proximal, the feather was scored "−." This occurred when the focal feather either was less advanced in its growth than the next distal feather, or when the focal feather was more advanced in its growth than the next proximal feather.

(3) If the focal feather was more advanced in its molt than both adjacent growing feathers, the feather was scored "ambiguous." This indicated that the focal feather was a series node. However, the direction of the molt series it started was ambiguous; molt could have progressed in either direction from such a feather.

(4) If the focal growing feather was surrounded by feathers that had not yet begun to be replaced, the feather was scored "?." These feathers give information about the location of series nodes—the feathers where a molt series was beginning—but the direction of molt cannot be inferred.

As Table 7 shows, in the outer series of feathers—from p10 to p6—molt nearly always proceeded from proximal to distal. Only in one out of 92 focal feathers did replacement in the outer series appear to be progressing from distal to proximal. For p1 to p5, molt always proceeded from distal to proximal, or else the direction was ambiguous; in no cases did feather replacement in the inner series progress from distal to proximal. This analysis shows that the patterns are not random: molt proceeds in two different directions. The middle primaries are most likely to be ambiguous nodes. For Laysan Albatrosses, p5 is the most ambiguous: p5 may either mark the beginning of an outer series or the beginning of an inner series. For Black-footed Albatrosses, the inner series more consistently begins at p5; only in two cases out of seven, rather than six cases out of six as for Laysan Albatrosses, could p5 be ambiguous.

WHICH SERIES OF PRIMARIES
GETS REPLACED?

There appear to be three distinct molt strategies of adult Laysan and Black-footed Albatrosses. Birds can replace all ten primaries in a single intensive molt, or they can replace only some of
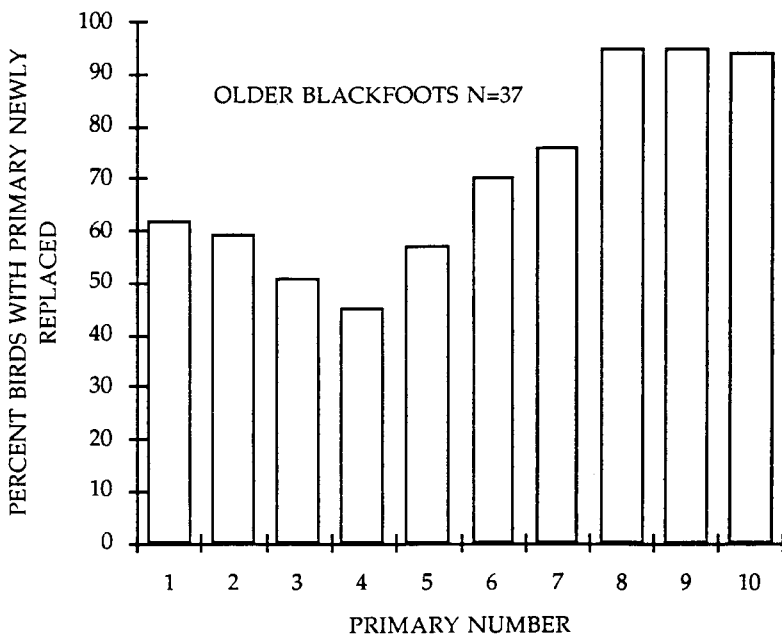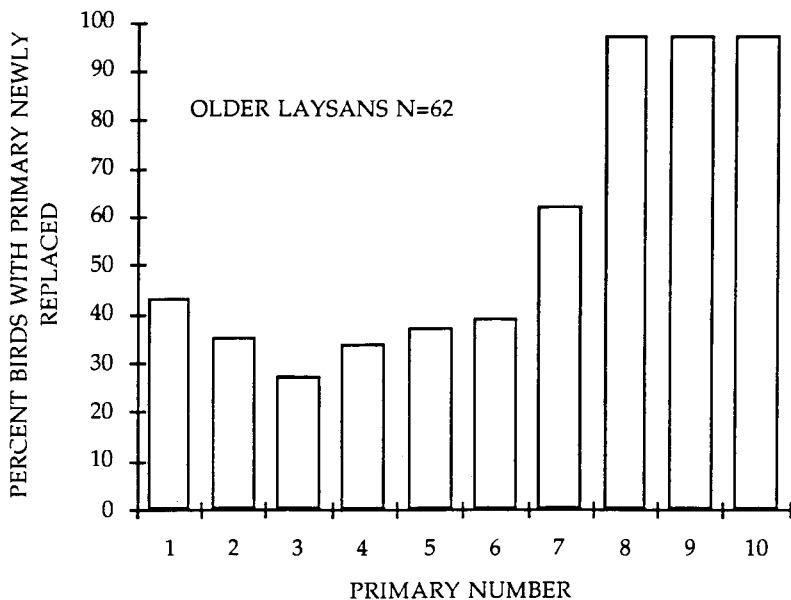
FIGURE 4. Molt in older birds: the probability of a feather having been replaced versus its position in the primary sequence. Includes birds finished molting or nearly finished molting.

their outer primaries and skip replacement of the inner primaries, or else they can replace some inners and some outer primaries. In any given year, 20% of older Laysan Albatrosses replace all 10 primaries, while 29% of older Black-footed Albatrosses do so (Table 8). As we show below, these are likely to be birds that failed their breeding attempt or skipped breeding entirely. Nearly

TABLE 6.   Molt patterns of all older birds with active inner series molt. 0 = newly replaced feather; 1 = feather replaced in the previous year's molt; 2 = feather replaced two molts before. Growing feathers are indicated by 0.X where X expresses the fraction of the feather already grown at the time of capture.

Bird ID#	Primary number									
	Inner primary series						Outer primary series			
	p1	p2	p3	p4	p5	p6	p7	p8	p9	p10
Laysan Albatross										
Mean primary length, mm ($n = 7$)	147	156	172	195	223	253	279	296	306	300
17	2	2	0.3	0.86	0.91	0.91	0.8	0.2	1	1
133	1	1	0.1	0.57	0.57	0.51	0.4	1	1	1
139	2	2	0	0.64	0.74	0.72	0.61	1	1	1
18	2	0.1	0.5	0.4	0.83	0.81	0.7	0.2	1	1
23	2	2	0.4	0.88	0.9	0.85	1	1	1	1
304	0.01	0.2	0.8	0	0	0	0.9	0.51	1	1
189		0.6	0.8	0	0	0	0	0.8	0.05	1
40	0.59	0.67	0.88	0	0	0	0.98	0.7	0.3	1
33	0.55	0.8	0	0	0	0	0.9	0.65	0.1	1
131	0.3	0.7	0	0	0	0	1	0.6	0.1	1
167	0.75	0.86	0	0	0	0	0	0.6	0.1	1
184	0.7	0	0	0	0	0	0	0.7	0.1	1
36	0.5	0	0	0	0	0	0	0.8	0.2	1
80	0.2	0.8	1	0	0	1	0.9	0.4	1	1
266	0.74	1	0	0	0	1	0	0	0.5	0.1
291	1	1	0.1	0.1	2	0.3	0.2	1	1	1
13	2	2	2	2	0.1	1	1	1	1	1
274	0.5	1	1	1	1	0	0.94	0.7	0.2	0.01
81	0.1	0.7	1	1	1	1	0.4	0.97	0.6	0.1
87	2	2	0.3	0.3	1	1		0.01	1	1
Black-footed Albatross										
Mean primary length, mm ($n = 7$)	147	157	173	196	226	257	281	303	311	299
12	2	2	2	2	0.66	0.69	0.69	0.54	1	1
145	2	2	2	2	0.17	0.22	0.1	1	1	1
171	2	2	2	0.88	0.91	0.85	0.69	0.1	1	1
16	2	2	2	0.8	0.85	0.9	0.1	1	1	1
25	2	2	0.96	0.96	0.99	0.98	1	1	1	1
289	0.01	0.35	0.89	0.89	0.9	1	0.65	0.2	1	1
98	0.2	0.59	0.8	0.8	0.96	2	0.78	0.29	1	1
154	2	0	0	0	0	0	0	1	0.9	0.3
306	2	0.1	0	0	0	0	0.97	0.28	1	1
84	0.83	1	1	1	0	0	0.1	0.93	0.42	1
97	0.2	2	0	0	0	0	0	0.8	0.2	0.2

half of the Laysan Albatrosses replaced only their outer series and skipped the inner series molt, while only 29% of Black-footed Albatrosses did this (Table 8). Less than one third of Laysan but 42% of Black-footed Albatrosses replaced some (but not necessarily all) inner series feathers. Birds replacing only their outer series replace a mean of 3.6 primaries ($n = 32$), while birds undergoing an inner series molt replace on average 8.2 primaries ($n = 47$).

OUTER SERIES MOLT

Older Black-footed and Laysan Albatrosses always replace at least p8, p9, and p10. The feather that begins outer series molt varies, but the end-point never varies: molt always proceeds to p10 without being arrested. Out of 83 Laysan and 55 Black-footed Albatrosses that were finished or nearly finished their molt when collected, only one bird violates this pattern.

Why do Laysan and Black-footed Albatross preferentially replace their outer series of primaries, instead of starting their molt with p1, the most common molt node for birds? The outer primaries of albatrosses become extremely worn, which may necessitate their annual replacement. We compared the feather wear scores of p1 and p10 for birds that had not yet begun their molt. We used only juveniles since all of their primaries are the same age. In Black-footed Albatrosses, the mean wear score of p10 was 1.84 ($n = 13$), versus 1.0 for p1 (Paired t value = 11.5, df = 12, p = 0.0001) while in Laysan Albatrosses, p10 has a wear score of 1.74 ($n = 10$) and p1 = 1.0 (Paired t value = 7.8, df = 9, P = 0.0001). We did not have enough pre-molting birds to compare the wear scores of p7 and p8, but it appears that there is a break in the degree of wear between the outermost three primaries and the remaining primaries.

Outer primaries wear more than inner primaries in most birds, but a glance at albatross wings shows this wear difference to be extreme, e.g., UWBM prep. numbers GWS 1215, BKS 334, BKS 337. This may be because they sometimes drag their wing tips in the water (Jeffrey Marks, pers. comm.). We presume they do so frequently enough that the outer primaries become far more abraded than inner primaries. Whatever its cause, the excessive wear of the outermost primaries makes a molt pattern that preferentially replaces them critical.

TABLE 7. Molt direction for primaries 1 to 10 in birds with actively growing primaries.

	Focal feather									
	Inner series					Outer series				
	p1	p2	p3	p4	p5	p6	p7	p8	p9	p10
Laysan										
+	—	0	0	0	0	4	11	25	26	25
—	9	7	7	4	0	0	1	0	0	—
Ambiguous	—	0	1	1	5	1	0	1	0	—
?	1	0	2	0	1	0	2	2	0	—
Black-footed										
+	—	0	0	0	0	3	7	12	9	12
—	2	2	5	5	5	0	0	0	0	—
Ambiguous	—	1	0	0	2	3	1	1	0	—
?	2	0	0	0	0	0	0	1	0	—

+: Number of cases where molt goes from proximal to distal.
—: Number of cases where molt goes from distal to proximal.
Ambiguous: Number of cases where molt could progress in either direction.
?: Number of cases where the growing focal feather is surrounded by unmolted feathers.

TABLE 8.   Differences between age and sex classes in molt patterns of albatrosses.

	Males	Females	Subadults	Adults	Total
			Laysan		
% Birds replacing					
Outer primaries only	42%	53%	49%	50%	49%
All ten primaries	26%	17%	20%	20%	20%
Some inner primaries	32%	29%	31%	30%	30%
	$\chi^2 = 1.3$, df $= 2$, $P = 0.5$		$\chi^2 = 0.03$, df $= 2$, $P = 0.9$		
			Black-footed		
% Birds replacing					
Outer primaries only	33%	27%	50%	19%	29%
All ten primaries	28%	29%	19%	33%	29%
Some inner primaries	39%	44%	31%	47%	42%
	$\chi^2 = 0.3$, df $= 2$, $P = 0.9$		$\chi^2 = 5$, df $= 2$, $P = 0.08$		

INNER SERIES MOLT

There are four curious things about the molt of the inner primary series. First, as shown above, replacement proceeds in the opposite direction from the outer primaries: from the middle primaries toward the body. Second, as we show below, p1 is often replaced on a schedule that associates it with the outermost secondaries rather than with the inner primaries. Third, molt occurs in the inner primaries only about once every two years and is usually incomplete. Thus,

TABLE 9.   The expected versus observed frequencies of primaries of different ages after one, two, or three molts, given a random model of feather replacement.

	Percentage of inner primaries of a given age, under a random model			
	New primaries	>1 year old	>2 years old	>3 years old
		Laysan		
After 1 molt	33.33%	66.67%	0.00%	0.00%
After 2 molts	33.33%	22.10%	44.80%	0.00%
After 3 molts	33.33%	22.10%	14.80%	29.60%
Expected	33.33%	36.95%	19.87%	9.87%
Observed	33.33%	62.00%	4.00%	0.00%
	$n = 248$ inner primaries, $\chi^2 = 66.7$, df $= 3$, $P = 0.0001$			
		Black-footed		
After 1 molt	50.00%	50.00%	0.00%	0.00%
After 2 molts	50.00%	25.00%	25.00%	0.00%
After 3 molts	50.00%	25.00%	12.50%	12.50%
Expected	50.00%	33.00%	12.50%	4.20%
Observed	50.00%	43.00%	1.30%	2.00%
	$n = 148$ inner primaries, $\chi^2 = 18.1$, df $= 3$, $P = 0.0004$			

old feathers accumulate in the inner series. Finally, molt of the inner primaries is organized adaptively, so that the oldest feathers are nearly always the first to be replaced. Given that all inner primaries are not molted every year, what are the possible patterns of inner molt? We describe and test four possibilities: random replacement, simple partial molt, stepwise molt, and wraparound molt.

Random replacement. We first considered the hypothesis that inner primary molt was random, so that birds would molt any inner feathers in a given year, not discriminating between old and new feathers. The directional replacement of inner primaries in our molting specimens excluded this as a possibility. Nonetheless, a random model seemed worth testing because other authors treating complex molt patterns have suggested they were irregular and without rules (Siegfried 1971, Stresemann and Stresemann 1966). We compared the actual feather ages in a population with the expected frequencies of feather ages that would result from a random model of molt. On average, Laysan Albatrosses replace one third of their inner primaries in any given year, while Black-footed Albatrosses replace 50% (from Fig. 4). Using a bifurcating tree with appropriate transitional probabilities, we then constructed expected frequency distributions of feathers that were new, one, two, or three years old. We did not allow more than three incomplete molts since birds appear to replace all 10 primaries every four years. In both species, the observed accumulation of two- and three-year-old feathers is considerably below the expected values generated by the random model (Table 9). This is as

we expect, if molt is orderly and designed to replace the oldest feather of a series first.

Simple partial molt. In the second model, simple partial molt, birds would begin with p5 and replace as many feathers as they can in sequence, stopping when they run out of time and next year starting at p5 again, not picking up where they left off. This simple pattern would produce an accumulation of older feathers at the end of the series (p2 and p1), and like random molt, would not differentiate between old and new primaries in the molt. Our evidence does not support this model. Albatrosses do not accumulate older primaries in p1 and p2, as would happen if inner molt always started at p5 and proceeded inward, stopping when the birds ran out of time and starting over again the next year at p5 without resuming molt where they left off (Fig. 4).

Stepwise molt. The third possibility is that albatrosses might molt their inner primaries by the rules of stepwise molt, which occurs when a second wave of molt begins before the first wave of molt has reached the end of a series, so that multiple waves of feather replacement proceed through a single series of feathers simultaneously. By definition, in stepwise molts the feather that begins the series (p1 in most birds, but p5 in the inner molt series of albatrosses) is replaced every molt. When the molt is incomplete in a given year, one wave of feather replacement starts at the series node in the next molt, and another wave starts with the next feather in any wave that did not reach the end of the series. Like simple partial molts, stepwise molts result in the seemingly maladaptive accumulation of old primaries among the last feathers of the series (Shugart and Rohwer, unpubl. ms.) but the effect is less extreme. In Laysan and Black-footed Albatrosses, 6 of 31 actively molting birds violate the predictions of stepwise molt since they did not initiate their molt at p5, the nodal feather for the inner series (Table 6, #291, #274, #81, #87, #84, #97). In birds finished with their molt, 5 of 60 had an older feather at p5 than p4–p1, which also violates stepwise molt. Nor did older feathers accumulate at the end of the series, as would be expected if Laysan and Black-footed Albatross replaced their inner series in a stepwise fashion (Fig. 4).

Wraparound molt. In large seabirds with incomplete molts, there should be strong selection for minimizing the accumulation of older primaries, since worn primaries are less efficient than new primaries. What pattern of inner feather replacement would assure that the oldest feathers are always the first to be replaced? The model our data support is best described as wraparound molt. In the first molt of inner primaries that follows a complete replacement of all primaries, molt is initiated at the beginning of the series, at p5. Should this molt wave be arrested before reaching the end of the series, in the next molt it simply picks up where it left off the year before. The critical distinction of wraparound molts is that the first feather of the series is not replaced again until the last feather of the series has been replaced.

In the following analysis, we omit p1 since, as we show below, p1 is sometimes part of the outer secondaries series. Thirty of 31 actively molting birds are consistent with wraparound (Table 6; #291 is the lone exception) and three birds clearly support the wraparound pattern and no other pattern (#274, #81, and #87). In these three birds, replacement of the inner series did not begin at p5, but instead at a primary further along in the series, which was presumably two or more years old before the molt began. Of birds finished with their molt, five more show that molt began not at p5, the beginning of the series, but rather further on in the series, because p5 is older than more proximal feathers. These birds also support the wraparound model. In sum, Laysan and Black-footed Albatrosses appear to minimize the accumulation of old inner primaries by having a single, wraparound wave of feather replacement that gives priority to replacing older feathers.

INNER PRIMARIES AND SECONDARIES

Molt of the inner series of primaries appears to have become disassociated with the molt of the distal primaries and linked with the molt of secondaries. The five inner primaries appear to be functionally more like secondaries than the outer primaries. As Table 7 shows, p1 and p2 are half the length of the three crucial outer primaries that are always molted, and basically the same length as the secondaries, which average 146 mm ($n = 7$). The inner primaries also show wear patterns like secondaries, not like outer primaries. As mentioned above, the mean feather wear score for p10 and p9 (measured on known age 1.5-year-old birds, only including feathers that were not growing and had not just been replaced) was 1.8 ($n = 28$) and 1.7 ($n = 11$) while the mean

feather wear score for p2, p1, s1, and s2 were all 1.01 ($n = 59$ for p1 and p2; $n = 54$ for s1, $n = 55$ for s2). Outer primaries are twice as long and get nearly twice the wear as the inner primaries, while the inners are about the same length and get the same wear as the secondaries. In most birds, and in the Laysan and Black-footed Albatrosses, the distal secondaries are molted from distal to proximal, just like the inner primaries.

Moreover, p1 is molted along with s1 more often than predicted by chance: in other words, they appear to be linked in their molt. We compared the number of adults with p1 and s1 having both new feathers, versus the number of adults with one feather new and one feather not new. Assuming that the only choices are new and one year old, the likelihood of finding them the same by chance would be 50%. Instead, in 74% of the adults that have finished molting, p1 and s1 are the same age ($n = 58$ adults; 35 Laysan and 23 Black-footed Albatrosses; the percentages of both species are exactly the same, so when species are combined, χ^2 with continuity correction = 13.2, $P < 0.001$, df = 1). Actually, since there are three possible ages for feathers: 0, 1, and 2; the probability of finding them both the same by chance = 33%, not 50%; this makes it far less likely that p1 and s1 were of similar age only by chance.

There are multiple foci of secondary molt, and molt of the secondaries occurs in short series. On average, there were 4.3 ± 0.5 foci of secondary molt for Laysans ($n = 20$ older birds with six or more actively growing secondaries); and for Blackfoots, 5.6 ± 0.5 foci ($n = 14$ older birds with six or more actively growing secondaries).

DISCUSSION

STEPWISE VERSUS WRAPAROUND MOLTS

Because we had noted a variety of feather ages in the wings of Laysan and Black-footed Albatrosses, we began this study to test the set of stepwise molt rules that hold for other large birds with incomplete primary molt. However, incomplete molts that produce alternating series of older and newer primaries within a single wing do not necessarily imply stepwise molt, as has often been assumed (Brooke 1981, Cooper 1985, Furness 1988, Harris 1973, Stresemann and Stresemann 1966). In this paper, we outline four possible patterns of incomplete molt for a single molt series: random molt, simple partial molt, stepwise molt, and wraparound molt. In *random*

molts, feathers are replaced randomly, and in *simple partial molts,* molt proceeds in a single wave that always starts at the first primary of a series. In *stepwise molts,* a second molt begins before the first wave of molt reaches the end of the series, so that multiple waves of feather replacement proceed through a single series of feathers simultaneously. With each initiation of molt, one wave of feather replacement starts at the first feather of the series, and other waves start where the previous year's molt ended. The term **wraparound molt** should be applied to a single wave of replacement proceeding in sequence through a single series. If the molt wave is arrested before reaching the end of the series, in the next molt it simply picks up where it left off the year before. The first feather of the series is not replaced again until the last feather of the series has been replaced. It is worth attempting to draw the distinction between stepwise molt and wraparound molt since stepwise molt produces the seemingly maladaptive accumulation of old feathers in the end of the series, while wraparound molt is far more efficient at replacing old feathers and conserving newer feathers.

One surprising result is that Laysan and Black-footed Albatrosses have bidirectional primary molt. With the exception of simultaneous molters, most birds treat all the primaries, which are defined as the morphological group of feathers inserting on the base of the hand, as a single molt series. Typically they begin molting with the most proximal primary and continue outward to the distal primary. We know of only one species, the Spotted Flycatcher (*Muscicapa striata*) that has reversed this pattern by starting its primary molt with the distal primary and molting inward (Stresemann 1963). Several genera of Falconidae and several owls have broken the primaries into inner and outer molt series which are replaced in op posite directions (Falconidae: Prevost 1983, Willoughby 1966, Miller 1941, Edelstam 1984; owls: Snowy Owl *Nyctea scandiaca*, Great Horned Owl *Bubo Virginianus*, Barn Owl *Tyto alba*; Stresemann and Stresemann 1966, Lenton 1984). However, these molts appear to always be complete. Many large raptors, herons, and seabirds have incomplete molts (Stresemann and Stresemann 1966, Ashmole 1968, Edelstam 1984), but these incomplete molts all appear to be unidirectional, progressing from p1 to p10; and to date, biologists have always interpreted these molts as belonging to a single series.

Why are Laysan and Black-footed Albatrosses different? An effect of reversing the directionality of inner primaries replacement is that inner series molt appears to have become disassociated with outer series molt and linked instead with replacement of the secondaries. Breaking the inner flight feathers into shorter series which are molted in a wraparound fashion means that feathers can be replaced more frequently. There will be limits as to how short these series can become, since each extra series increases by one the number of feathers (or adjacent groups of feathers) simultaneously growing. A perhaps fortuitous effect of reversing the directionality of the molt of the inner primaries is that this makes it possible to break the entire inner series of flight feathers (inner primaries and outer secondaries) into multiple wraparound series. As we show, p1 is more often part of a molt series involving the outermost secondaries than it is part of the inner primary molt series. This idea of multiple wraparound series involving inner primaries and secondaries should be pursued by analyzing the rules of feather replacement in the secondaries: the direction of molt, the length of the series, the number and location of nodes, and so forth. We recognize that the adaptive logic of breaking inner primaries and secondaries into an optimal number of wraparound molt series presumes a prior reversal in the order of replacement of the inner primaries. We have no convincing selective argument to offer for this change.

PATTERNS IN OTHER ALBATROSSES

In large seabirds that cannot complete an entire flight feather molt in one year, selective pressures for efficient molt patterns should be strongest in species where time is most constrained. All albatrosses are long lived, lay only one egg a year, and have prolonged breeding seasons. The system appears to be driven by the development time of the single egg clutch, which may have evolved to allow for heightened immune systems in these long lived birds (Ricklefs 1993). Whatever the reasons for prolonged development time, the result is a striking time constraint on other activities. No albatross combines molting with breeding (Brooke 1981, Furness 1988), and all of the albatrosses examined to date show incomplete molts. We predict that albatrosses in general should show similar patterns of molt.

Data on albatross molt is sparse, but the evidence suggests that other species show complex patterns of molt similar to Laysan and Black-footed Albatrosses. Yellow-nosed Albatrosses (*Diomedea chlororhynchos*) replace their inner primaries less frequently than their outer primaries (Furness 1988), which suggests that they too may follow molt rules similar to those described here. Furness (1988) also noted that primary replacement was not random in Yellow-nosed Albatrosses, since although only about half the primaries were renewed each year, very few feathers were retained for more than two years. An annual tropical breeder, the Waved Albatross (*D. irrorata*) may also follow similar rules. By examining breeders, Harris (1973) concluded that the outer primaries were replaced annually and inner primaries less often. Rechten (1986) has shown that successfully breeding Waved Albatrosses do not appear to have quite enough time in a year to complete the breeding cycle, molt, and return in time to breed successfully, again suggesting that there are strong time constraints on this species as well. Waved Albatrosses that failed in their breeding attempt replace 9.8 — nearly all — their primaries before they breed again (Prince et al. 1993), a pattern that corresponds to what we predict for the Laysan and Black-footed Albatrosses.

Brooke and Furness (1982) found three specimens of the annually breeding Black-browed Albatrosses (*D. melanophris*) with what they called ascendent molt: molt proceeding from outer to inner, suggesting that this annually breeding species might show patterns similar to that of the Laysan and Black-footed Albatrosses. Black-browed and Shy Albatrosses, both annual breeders, show incomplete molt (Melville 1991), but not stepwise molt since numerous specimens have old inner primaries but newly replaced, or actively growing, outer primaries. Unfortunately, none of Melville's specimens were growing inner primaries, so it is difficult to tell whether these two species show the same molt patterns as Laysan and Black-footed Albatrosses.

Prince et al. (1993) examined molt in Black-browed (*D. melanophris*) and Grey-headed Albatrosses (*D. chrysostoma*) during the breeding season, using banded birds whose past breeding histories were known in detail. Both species are sub-Antarctic breeders; the Grey-headed is resident in high latitudes year round and is a biennial breeder, while the Black-browed winters in warm waters off South Africa and breeds annually. Using birds that had completed their molt,

Prince et al. found that both species had broken their primaries into two series, which were replaced in opposite directions. Every other year, birds replaced their outer three primaries (from proximal to distal) and some of their inner primaries (from distal to proximal) — a pattern strikingly similar to that shown by Laysan and Black-footed Albatrosses. However, unlike the Laysan and Black-footed Albatrosses, in alternate years the Black-browed and Grey-headed Albatrosses replaced none of the outer three primaries, but instead replaced the middle primaries (5, 6, and 7) and some of the inner primaries. After eight years or so, the Black-browed Albatross has reached a pattern which ensures that about half the primaries are replaced each year. In contrast, the Grey-headed Albatross replaces fewer than half the primaries each year, and as a result worn feathers can accumulate in the inner primaries: some birds go five years before replacing certain inner primaries.

Laysan and Black-footed Albatrosses show a pattern of incomplete molt in their primaries which has never before been described for any bird. Juvenile Laysan and Black-footed Albatrosses replacing their flight feathers for the first time replace only their distal three or four primaries. Nearly half the adults do the same thing as the juveniles: confine their molt to the outer three primaries. However, eventually they do have to replace the inner series of feathers. The two series of primaries are replaced in opposite directions and follow different rules for determining feather replacement. The distal series always molts in a single wave, and which feather initiates molt is not fixed, but determined by the time they have available to molt. At least the outermost feathers of the outer series are molted every year without fail. The inner series are also molted in a single wave, but in a wraparound fashion.

Adults replace their primaries in one of three patterns: they may molt all ten primaries; they may molt only the outer series, replacing some or all of the five outer primaries; or they may molt the inner series as well as the outer series, replacing some or all of the inner primaries. Molt of some inner series primaries occurs only in one third of the Laysan Albatrosses and half of the Black-footed Albatrosses each year. In other studies, we argue that these individual differences correlate with variation in condition and time available for molting.

The complex molt pattern which Laysan and Black-footed Albatrosses have evolved seems to avoid many of the problems associated with stepwise molts. In stepwise molts, the oldest feathers are not the first to be replaced and old, worn out feathers accumulate among the outermost primaries. By creating a separate outer series and always replacing the outermost primaries of this series, old feathers do not accumulate in the outer part of the wing. Molting the inner series in a wraparound fashion insured that the oldest feather of this series is always the next to be replaced.

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