EVALUATION OF MOLT SEQUENCES AND STRATEGIES IN ALBATROSSES BASED ON REPLACEMENT OF JUVENILE REMIGES

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ABSTRACT

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Albatrosses have long been known to undergo complex replacement strategies among primaries, including "Staffelmauser" or stepwise molt, here expanded in definition to include replacement patterns among multiple series of primaries. Interpreting primary replacement sequences for birds undergoing Staffelmauser can be complicated by multiple molt waves, which have led to conflicting opinions on the sequences of primary replacement in albatrosses. In order to determine replacement sequences in such cases, it is necessary to examine molt of the first set of juvenile remiges, but this occurs entirely at sea in albatrosses and is thus poorly documented. Here, to clarify molt sequences, I canvassed over 63,000 images in the Cornell Lab of Ornithology's Macaulay Library and located 156 albatrosses that were molting juvenile primaries or showing mixed juvenile and basic feathers. These included 14 taxa in three genera, restricted to those in which the age of younger birds could be inferred from plumage, bill color, and/or iris color. Distal replacement of the three juvenile outer primaries (p8–p10) occurred consistently in all birds. Based on replacement of juvenile primaries, I define three molt series: p8 distally to p10, p1 distally to p3, and a series in which replacement can commence either at p7 and proceed proximally to p4 or at p6 and proceed bidirectionally to p7 and p4. In the third series, the commencement node appears to be fluid between p6 and p7, as has been proposed for nodes in other bird taxa. Other elements of albatross molt strategies besides sequence—such as timing, location, extent, and replacement rates within each molt series—appear to be less fixed. In particular, initial replacement of remiges may occur at either the first or the second prebasic molt both among and within taxa, varying in part according to primary lengths. I predict that the fixed molt series described here will occur across all taxa of Diomedeidae, but that the timing and extent of each molt will vary more widely within and among taxa, making it challenging to define precise molt cycles in albatrosses.

Key words: *Diomedea*, Macaulay Library, *Phoebastria*, Staffelmauser, *Thalassarche*

INTRODUCTION

"Staffelmauser," or "stepwise molt," is a prebasic molting strategy in large birds, during which the initiation of a molt series among primaries can commence before the previous series has completed, resulting in multiple waves of primary replacement (Dorward, 1962; Howell, 2010; Pyle, 2006; Stresemann & Stresemann, 1966). It typically occurs in large birds that lack the time to complete replacement of all primaries during a single molt, given other annual-cycle energy constraints, e.g., those related to breeding and migration. Although the proximal cause of Staffelmauser appears to be lack of time to molt, it also has the ultimate benefit of allowing more primaries to be replaced annually without incurring large, flight-inhibiting gaps in the wings (Pyle, 2005; Shugart & Rohwer, 1996).

Staffelmauser has largely been documented among birds that undergo a typical distal molting sequence from the innermost (p1) to the outermost (p10) primary, resulting in two or more waves of active replacement (e.g., Dorward, 1962; Howell, 2010; Pyle, 2005, 2006; Stresemann & Stresemann, 1966). Here I propose extending the definition of Staffelmauser to similar processes within other series of primaries in bird families in which molt is not strictly distal, such as those of herons and egrets (Pyle, 2008; Shugart & Rohwer, 1996), owls (Pyle, 2022a; Stresemann & Stresemann, 1966), and parrots (Guallar et al., 2025; Pyle, 2013). I further propose applying Staffelmauser to molt series among secondaries, occurring within most or all species that exhibit Staffelmauser among primaries (Pyle, 2006, 2008), as well as to primary coverts when they molt separately from primaries, as documented thus far in flamingos, kingfishers, woodpeckers, and parrots (Guallar et al., 2025; Jenni et al., 2026; Pyle, 2022a; Pyle & Schofield, 2024; Shannon, 2000). Each of these tracts appear to show fixed replacement sequences within families that can be subject to Staffelmauser, i.e., with a new molt series commencing before the prior series has completed (Pyle, 2013; Pyle & Schofield, 2024).

Albatrosses undergo annual prebasic molts that can vary in timing and sequence with breeding activity. Older birds may skip a year of breeding when there is a need for more molting, and larger species can breed on a biennial cycle that allows for two prebasic molting periods between breeding seasons (Edwards, 2008; Prince et al., 1993, 1997). Molts in pre-breeding birds, up to 3–6 or more years of age, occur entirely at sea and are poorly understood but presumably include a second prebasic molt about one year after fledging, followed by annual prebasic molts thereafter (Howell, 2010, 2012; Pyle, 2008). Molt timing and extent appear to vary considerably among individuals during prebasic molts, which can be protracted throughout the year in non-breeding birds. During the second and later prebasic molts, individuals may replace anywhere from none, a few, to perhaps all primaries.

Albatrosses have long been known to undergo complex replacement strategies among primaries. Stresemann and Stresemann (1966), Brooke (1981), and Melville (1991) recognized that Staffelmauser (or "wave molt") occurred in albatrosses but concluded that it proceeded in a simple distal (or "descendant") sequence from the innermost p1 to the outermost p10, or they were unclear on replacement patterns. Langston

and Rohwer (1995) ascertained that multiple series occurred and proposed that a distal series occurred from p6 to p10 and a proximal series from p5 to p1. Further, they proposed that a Staffelmauser-like or "wrap-around" process occurred within the inner series following incomplete molts. Subsequent authors (e.g., Catry et al., 2013; Howell, 2006; Jiguet, 2000; Prince et al., 1997; Ryan & Adekola, 2023) recognized that p6 and p7 could be more aligned with the inner than the outer series. Most of these authors assumed that the inner series was proximal ("ascendent") beginning with p7. However, several studies also document that the innermost primary, p1, was replaced before other primaries in the inner series, some inferring that this initiated a distal sequence (*cf*. Howell, 2006). Langston and Rohwer (1995) and Edwards and Rohwer (2005) explained the replacement of p1 by linking it with that of the secondaries and also attributed other anomalies to primaries being skipped in sequence. However, both of these factors would involve unique molting strategies in birds that would require more rigorous testing to confirm.

Most data on molt sequences and extent in albatrosses have been inferred from replacement patterns on breeding adults at colonies (e.g., Catry et al., 2013; Prince et al., 1993, 1997) or are based on replacement extent (but not sequence) following molts of juvenile feathers in birds by-caught at sea (Bugoni & Furness, 2009; Edwards & Rohwer, 2005; Langston & Rohwer, 1995; Ryan & Adekola, 2023). The problem with inferring molt sequences in older (adult) birds that undergo Staffelmauser is that replacement within a series can involve more than one molt wave, resulting in irregular or even opposite between-feather sequences to those of original directionality after several years of replacement. For example, a wave "catching up" to another wave among primaries can result in false suppositions about sequence or that a primary had been skipped. In order to accurately infer series and replacement sequences, it is necessary to examine molt sequences during replacement of the first set of juvenile remiges, which can take up to four or five years to complete in albatrosses (Prince et al., 1993, 1997; Pyle, 2008). Because few birds of these ages (known age or otherwise) return to colonies, no previous study has accurately confirmed molt directionality of juvenile primaries in albatrosses.

In smaller albatrosses of the Northern Hemisphere (within genus *Phoebastria*), replacement of the juvenile p8–p10 is reported to occur invariably during the second prebasic molt at about one year of age, often along with some primaries among p1–p7. Most or all primaries are replaced by the third prebasic molt, during which p8–p10 are replaced again (Howell, 2012; Langston & Rohwer, 1995; Pyle, 2008; Rohwer & Edwards, 2005).

In albatrosses of the Southern Hemisphere (e.g., among genera *Thalassarche* and *Diomedea*), molt of primaries has been reported to occur in alternating annual patterns, with the outer series (p8–p10) and occasionally one or two additional primaries invariably replaced during the third prebasic molt and those among p1–p7 invariably replaced during the fourth prebasic molt (Howell, 2010, 2012; Jiguet, 2000; Prince et al., 1993, 1997; Ryan & Akedola, 2023). These two "phases" (defined as Phase 1 and Phase 2, respectively) are reported to alternate in sequence biennially, at least until breeding commences at age 6–10 y or later. This has, in turn, led to the reported ability to precisely age southern albatrosses in their first few cycles based on molt phase along with other age-related criteria such as bill color and plumage patterns (e.g., Bugoni & Furness, 2009; Flood, 2014; Flood et al., 2015; Flood & Ryan, 2018; Howell & Zufelt, 2019; Jiguet, 2000; Prince & Rodwell, 1994; Pyle, 2008). As smaller species of *Phoebastria* are reported to molt p8–p10 every year, phases have not been defined for those species. However, molt extent in large birds is rarely this invariable or predictable (*cf*. Pyle [2008], regarding condors, pelicans, owls, and other large birds). In albatrosses, the extent of prebreeding-age molts can vary substantially due to food-resource availability during molting periods (e.g., Cobley & Prince, 1998). Prince et al. (1993) present compelling data for fixed every-other-year replacement in the Black-browed Albatross *Thalassarche melanophris*, as described above. However, their conclusions were based primarily on molt patterns in adults returning to the colony for the first time at ages 3–10 yr, and some of their results on younger birds appear contradictory (e.g., two-year-old birds appeared to be assigned Phase 1, whereas birds in Phase 2 were reported to be 18 months old), perhaps because age was inconsistently defined as time since hatching or time since fledging (see below). Jiguet (2000) also infers that two-year-old Black-browed Albatrosses have already molted p8–p10, and Flood and Ryan (2018) caution that some birds in genus *Thalassarche* may follow non-alternating strategies or show similar molt timing to that of genus *Phoebastria*. Invariable replacement of p8–p10 during the second prebasic molt in *Phoebastria* and during the third prebasic molt in *Thalassarche* and *Diomedea* has otherwise been based on presumed ageing by maturation of plumage and bill coloration, which has also been inferred to be variable among individuals (Bugoni & Furness, 2009; Flood & Fisher, 2015; Flood & Ryan, 2018; Jiguet, 2000). Circular reasoning or over-prioritizing molt patterns over other age-related criteria may thus have confounded interpretations of alternating molt schedules in these albatrosses, including the molt cycle in which p8–p10 are initially replaced.

Among secondaries, there is agreement that replacement occurs in both directions, distally from the tertials and proximally from the outermost secondary, s1 (summarized by Ryan & Akedola, 2023). However, there is disagreement about whether or not there is also a distal node at the fifth feather from the outside (s5), which often occurs among dyastataxic species such as albatrosses. Stresemann and Stresemann (1966) and Brooke (1981) inferred that a node was lacking at s5, whereas Pyle (2008) assumed that a node was present at s5.

To clarify replacement sequences and timing of juvenile primaries and secondaries, I examined images of 14 taxa among three albatross genera catalogued at Cornell Lab of Ornithology's Macaulay Library. At the time of this study, the Macaulay Library contained over 75 million images of birds. Effective use of this catalogue to study molts in birds has been demonstrated (Pyle, 2022b), as has the effective use of photographs to study molt in albatrosses (Osborn & Ryan, 2021).

METHODS

The number of species and subspecies of albatrosses is currently debated. I examined Macaulay Library images, catalogued as of July 2025, among 14 taxa in four groups within three genera. I considered sample sizes, accuracy in identifications among Macaulay Library images, and taxa for which age (molt cycle) could be independently assessed by plumage and/or bill coloration: the "Great Albatrosses" (*Diomedea*, including species or subspecies *sanfordi*, *epomophora*, *exulans*, *dabbenena*, *antipodensis*, *gibsoni*, and *amsterdamensis*; *ca*. 15,500 images); the "Shy Albatrosses" *Thalassarche* (including species or subspecies *cauta*, *steadi*, *salvini*, and *eremita*; *ca*. 16,000 images); the Black-browed Albatrosses *Thalassarche* (including species or subspecies *melanophris* and *impavida*; *ca*. 17,000 images); and the monotypic Black-footed Albatross *Phoebastria nigripes* (*ca*. 15,000 images). Within each of these groups I checked categories

of both identified and unidentified taxa that are recognized by the Macaulay Library. Grouping the above taxa as such precludes widespread concerns about identification of species or subspecies within these taxa when observed at sea away from breeding colonies.

I ordered images from oldest to newest date of observation, and I included only one datum per date, location, and age/plumage category to reduce sampling the same bird more than once (see Pyle, 2022b). When multiple images of the same bird were available, I used all images to collect the most accurate data for that individual. I screened the images for birds with fully extended wings in which all primaries were visible on at least one wing. I exported and enlarged potentially usable images with a photo-editing program for detailed assessment. I scored the condition of each primary as juvenile, growing, or basic. For basic primaries, I carefully assessed the direction of molt between each pair of adjacent primaries based on either the length of growing feathers when actively molting or by "molt clines" (Pyle, 2005, 2008), i.e., by determining which feather was newer and hence had been replaced later than the adjacent feather of the pair. Directionality between each pair of adjacent primaries was scored as "distal," "proximal," or "similar." The last category was assigned when the adjacent primaries were similar in length during active molt or in degree of wear, indicating that they had molted at the same time or close to it.

The identification of juvenile primaries was based on their narrower and more tapered shapes, more extensive wear and bleaching than retained basic feathers, and lack of molt clines indicating prior sequential replacement (Pyle, 2008; juvenile feathers are grown synchronously at the natal location). Age of feather generations and molt cycle was also inferred in combination with bill color and pattern in the two *Thalassarche* species, iris color in Black-browed Albatross subspecies *impavida*, and body-feather coloration and retention patterns of juvenile secondaries and/or secondary coverts in all taxa (Bugoni & Furness, 2009; Flood, 2014; Flood et al., 2015; Flood & Ryan, 2018; Howell, 2010, 2012; Howell & Zufelt, 2019; Jiguet, 2000; Pyle, 2008). In some cases, when all primaries were either growing or basic, I aged the birds based on a block of retained juvenile secondaries between s7 and s17, following the retention patterns summarized by Pyle (2008) and Ryan and Akedola (2023), and indicating that at least some juvenile primaries had been replaced during the previous molt. I also noted birds of these taxa that were undergoing active replacement of basic primaries and showed plumage and bill coloration characteristic of older birds, in order to infer timing of this molt in breeding-age individuals of each species. Replacement patterns of juvenile and basic secondaries were noted when visible.

Based on the age-determination criteria described above, the freshness of juvenile primaries, and replacement patterns among secondaries and secondary coverts, I attempted to assign each bird to its molt cycle, categorizing individuals as undergoing the second, third, fourth/fifth, or later prebasic molt or as being in the second, third, or fourth/fifth plumage cycle. By the fourth and fifth cycles, precise ageing was deemed unreliable due to the potential for overlap between cohorts in molt patterns and other age-related criteria (*cf*. Pyle, 2008); therefore, these two age categories were combined. I thus attempted to categorize each bird that was molting or had replaced p8–p10 for the first time (i.e., the initial Phase 1) to the second, third, or fourth/fifth molt cycle. A few birds showed conflicting characters between primary freshness and other age criteria. In these cases, I assigned molt cycle as accurately as possible, but age assignments and interpretations of molt cycles for these individuals should be considered tentative (see Discussion).

Ages were classified as months since fledging rather than since hatching, following Howell (2010, 2012). These age definitions can differ by up to six months in smaller albatrosses and up to eight months in larger taxa. This classification reflects the approximate age since completion of the prejuvenile (first prebasic) molt. Here, the second prebasic molt is assumed to occur around 8–12 months since fledging (up to 18–21 months after hatching), with subsequent prebasic molts occurring at approximately annual intervals following the second prebasic molt (Howell, 2010, 2012; Pyle, 2008). I also considered the possibility that timing of molts may vary in years when breeding is skipped or in species with biennial breeding cycles (Flood & Ryan, 2018; Prince et al., 1993, 1997). Specific Macaulay Library images are referenced as "ML" followed by the unique numeric identifier of each image.

RESULTS

I canvassed over 63,000 images and identified 156 albatrosses that were molting juvenile primaries or showed mixed juvenile and basic remiges (Table 1). Sample sizes among genera ranged from 44 Shy Albatrosses to 80 Great Albatrosses. Sixty birds were actively molting and 96 were not molting but showed mixed

TABLE 1
Sample size distributions for 156 albatrosses molting juvenile primaries or having mixed juvenile and basic remiges

	2nd prebasic molt[a]	2nd basic plumage[a]	3rd prebasic molt[a]	3rd basic plumage[a]	4th/5th prebasic molt[a]	4th/5th basic plumage[a]	Total
Great Albatrosses[b]	0	2	5	27	8	20	**62**
Shy Albatrosses[c]	1	2	5	7	1	2	**18**
Black-browed Albatrosses[d]	2	5	7	13	5	7	**39**
Black-footed Albatross[e]	14	8	9	3	3	0	**37**
TOTAL	**17**	**17**	**26**	**50**	**17**	**29**	**156**

[a] Note the categorization by the second, third, and fourth/fifth basic cycles should be considered provisional (see text).
[b] Great Albatrosses *Diomedea* (including species or subspecies *sanfordi, epomophora*, *exulans*, *dabbenena*, *antipodensis*, *gibsoni*, and *amsterdamensis*)
[c] Shy Albatrosses *Thalassarche* (including species or subspecies *cauta*, *steadi*, *salvini*, and *eremita*)
[d] Black-browed Albatrosses *Thalassarche* (including species or subspecies *melanophris* and *impavida*)
[e] Black-footed Albatross *Phoebastria nigripes*

juvenile and basic remiges. Sample sizes of actively molting birds ranged from 17 for each of the presumed second and fourth/fifth prebasic molts to 26 for the presumed third prebasic molt. Sample sizes for plumages ranged from 17 for presumed second basic plumage to 50 for presumed third basic plumage (Table 1).

Molt Extent During the Second to Fifth Molt Cycles

Of the 156 albatrosses with juvenile primaries, 83 were judged to be undergoing or to have completed only one prior molt of primaries (all "Phase 1" for the larger species), 50 were judged to have undergone two replacements (predominantly "Phase 2" for the larger species), and 23 were judged to have undergone three replacements (predominantly "Phase 1" for the larger species). In all 83 cases, the first molt of primaries included replacement of p8–p10, with no evidence that only one or two of these juvenile feathers were replaced. Likewise, there was no evidence of partial replacement of p8–p10 during the second or third replacements of these feathers (n = 73).

Based on an independent assessment of wear and bleaching of unmolted feathers, together with other age-determination criteria,

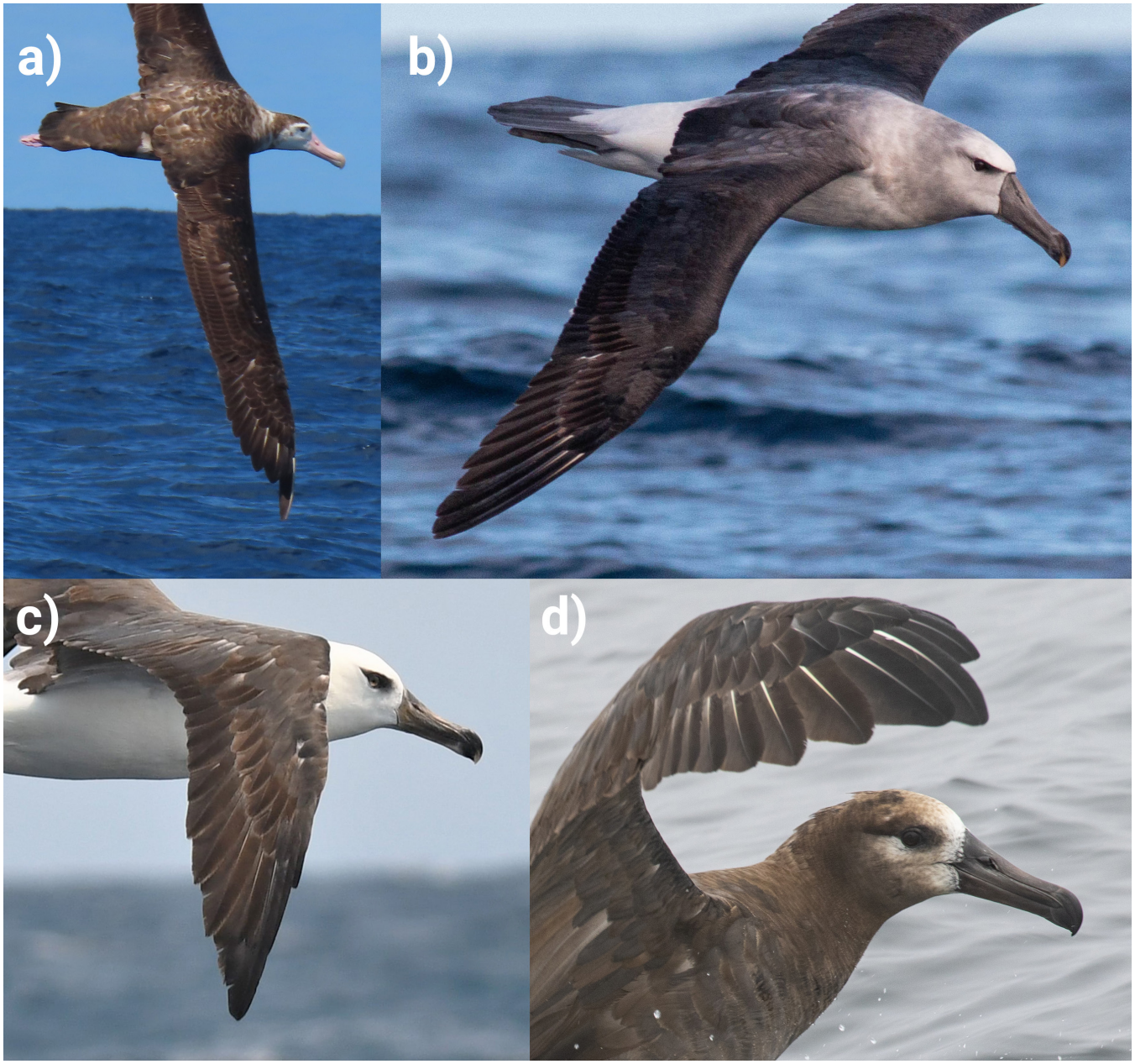

Fig. 1. Albatrosses that may be replacing or have replaced primaries for the first time during the second prebasic molt, based on bill coloration, iris color, plumage, freshness of unmolted juvenile primaries, and/or minimal replacement of secondaries and/or secondary coverts (see text): (A) Great Albatross *Diomedea* sp., 16 Sep 2023 (see also ML615904805); (B) Shy Albatross *Thalassarche* sp., 19 Jun 2022 (see also ML429854251, ML614473046, ML621394759, and ML629057225); (C) Black-browed Albatross *Thalassarche* sp., 28 Dec 2019 (see also ML598283121, ML347913021, ML6284018660, ML588865671, and ML624636245); and (D) Black-footed Albatross *Phoebastria nigripes*, 26 Aug 2022 (note p7 also replaced and fresher than p8). Photo credits: © Jemaine Mulcahy (A, ML608880024), Pedro Nicolau (B, ML460850571), Trevor Ross (C, ML347913021), and Simon Lane (D, ML487980921)

I tentatively judged first replacement of p8–p10 to occur during the second prebasic molt for 34 albatrosses (two Great, three Shy, seven Black-browed, and 22 Black-footed Albatrosses; Table 1, Fig. 1) and during the third prebasic molt in 64 albatrosses (32 Great, 12 Shy, and 20 Black-browed but no Black-footed Albatrosses; Table 1, Fig. 2). No albatrosses were deemed to have retained the juvenile p8–p10 until the fourth prebasic molt. However, this would have been difficult to infer using the criteria assessed, and some albatrosses with very worn juvenile primaries and more advanced bill and plumage characters may have done so (Fig. 2c; see also ML140344751, ML490555021, ML208185081, ML626372187).

For 63 of 83 birds, the first replacement of primaries included only p8–p10; for the remaining 20 birds, additional primaries were replaced. These included p1 (14 birds), p7 (12 birds), p2 (four birds), and p6 (two birds); no birds had replaced p3–p5

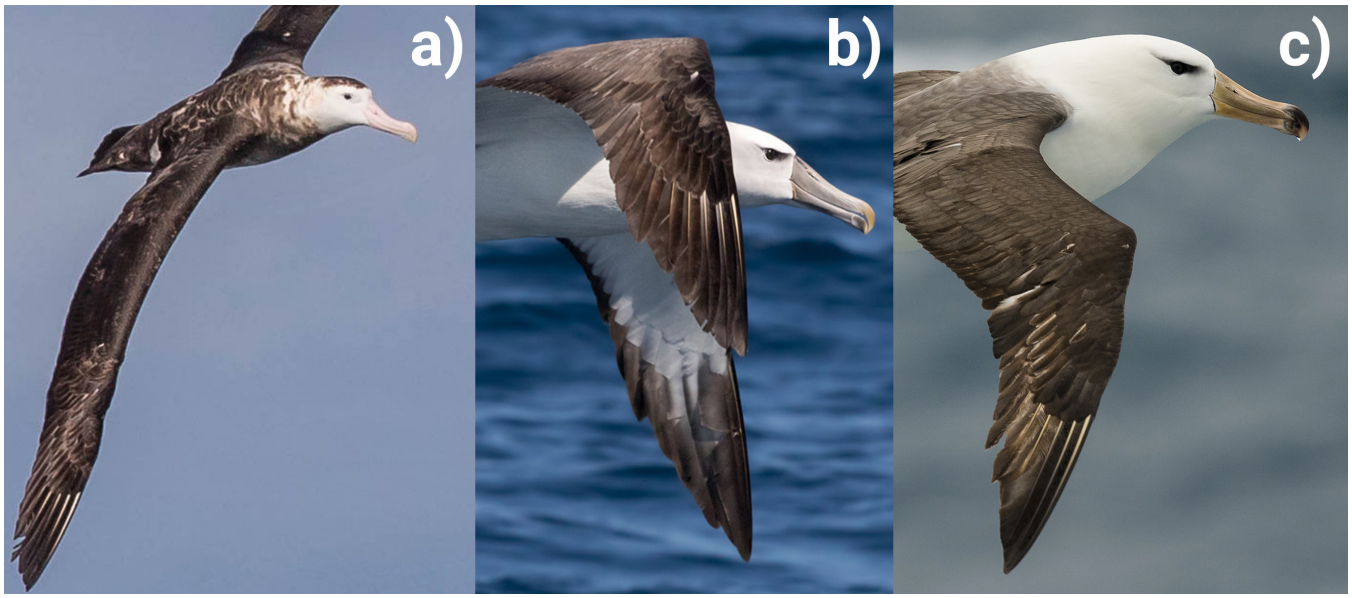

Fig. 2. Albatrosses replacing or having replaced primaries for the first time during the third prebasic molt, based on bill coloration, iris color, plumage, wear of unmolted juvenile primaries, and a greater replacement extent of secondaries and secondary coverts (see text): (A) Great Albatross *Diomedea* sp., 05 May 2019 (see also ML493285121, ML455125781, ML419492111); (B) Shy Albatross *Thalassarche* sp., 05 Nov 2018 (see also ML629057219, ML608636930, ML621394759, ML629057219); (C) Black-browed Albatross *Thalassarche* sp., 16 Jan 2019 (see also ML627767896, ML76588731, ML628172497). The bird in (C) shows very worn retained juvenile primaries (p2–p7), somewhat advanced bill coloration, and apparent replacement of most secondaries and secondary coverts, perhaps indicating first replacement of p8–p10 at the fourth prebasic molt; alternatively, it may show remiges that became worn at a quicker rate than those of other individuals. Photo credits: © Kevin Bartram (A, ML275702621), Lars Petersson | My World of Bird Photography (B, ML206002941), and Ian Routley (C, ML140344751)

TABLE 2
Replacement patterns of juvenile inner primaries (p1–p7) during the inferred second and third prebasic molts in albatrosses

Taxon	p1	p2	p3	p4	p5	p6	p7
a) p8–p10 first replaced during the second prebasic molt[a]							
Great Albatrosses[b] (*n* = 2)	0	0	0	0	0	0	0
Shy Albatrosses[c] (*n* = 4)	1	0	0	0	0	0	0
Black-browed Albatrosses[d] (*n* = 8)	0	0	0	0	0	0	0
Black-footed Albatross[e] (*n* = 47)	6	2	0	0	0	2	9
b) p8–p10 first replaced during the third prebasic molt[a]							
Great Albatrosses[b] (*n* = 27)	0	0	0	0	0	0	2
Shy Albatrosses[c] (*n* = 10)	4	0	0	0	0	0	0
Black-browed Albatrosses[d] (*n* = 10)	4	2	0	0	0	0	1
TOTAL	**14**	**4**	**0**	**0**	**0**	**2**	**12**

[a] Note that the assignment of these molts should be considered provisional (see text).
[b] Great Albatrosses *Diomedea* (including species or subspecies *sanfordi, epomophora*, *exulans*, *dabbenena*, *antipodensis*, *gibsoni*, and *amsterdamensis*)
[c] Shy Albatrosses *Thalassarche* (including species or subspecies *cauta*, *steadi*, *salvini*, and *eremita*)
[d] Black-browed Albatrosses *Thalassarche* (including species or subspecies *melanophris* and *impavida*)
[e] Black-footed Albatross *Phoebastria nigripes*

(Table 2). Black-footed Albatross accounted for 19 of these 32 replaced primaries (*cf*. Fig. 1d), including the only species to have replaced p6 (Table 2). Among the other taxa, one Shy Albatross had replaced p1 during what was inferred to be the second prebasic molt (ML106507411), and the remaining 11 primary replacements occurred after the inferred third prebasic molt in which p8–p10 were initially replaced (Table 2). Examples of the latter include ML208234511 and ML455125781 (Great Albatrosses); ML490555021, ML608636930, and ML613090241 (Shy Albatrosses); and ML140344751, ML6075511361, ML627767896, and ML630058124 (Black-browed Albatrosses).

Sequence of Primary Replacement

The proportions of distal, proximal, or similar replacement sequences between each pair of juvenile primaries is presented in Figure 3. Distal replacement from a node at p8 was inferred in all 156 cases, with no evidence that p9 was replaced before p8 or that p10 was replaced before p9, indicating a consistent distal series from p8 to p10. In one case (Black-footed Albatross ML625483485), p7 and p8 were judged to have been replaced at the same time during the second prebasic molt. In the remaining 82 cases, p7 was replaced after p8, during either the same or the subsequent prebasic molt.

A node at p1 with distal replacement to p2 was recorded for all 74 cases in which this sequence could be evaluated, and distal replacement from p2 to p3 was recorded in all 48 such cases (*cf*. Figs. 3, 4). Replacement sequences among p5 to p7 were more variable (Fig. 3). Replacement of p6 subsequent to p7 (proximal replacement) was judged to have occurred during 29 of 73 cases, p6 and p7 were judged to be replaced at about the same time in 25 cases, and p6 was judged to be replaced prior to p7 (distal replacement) in 19 cases. Replacement of p5 was judged to either follow that of p6 (proximal replacement; 44 cases) or to be replaced at about the same time as p6 (15 cases). In all cases (n = 38), replacement of p4 was judged to follow that of p5 (Fig. 3). Examples of albatrosses illustrating replacement sequences among p4–p7 are shown and discussed in Figure 5.

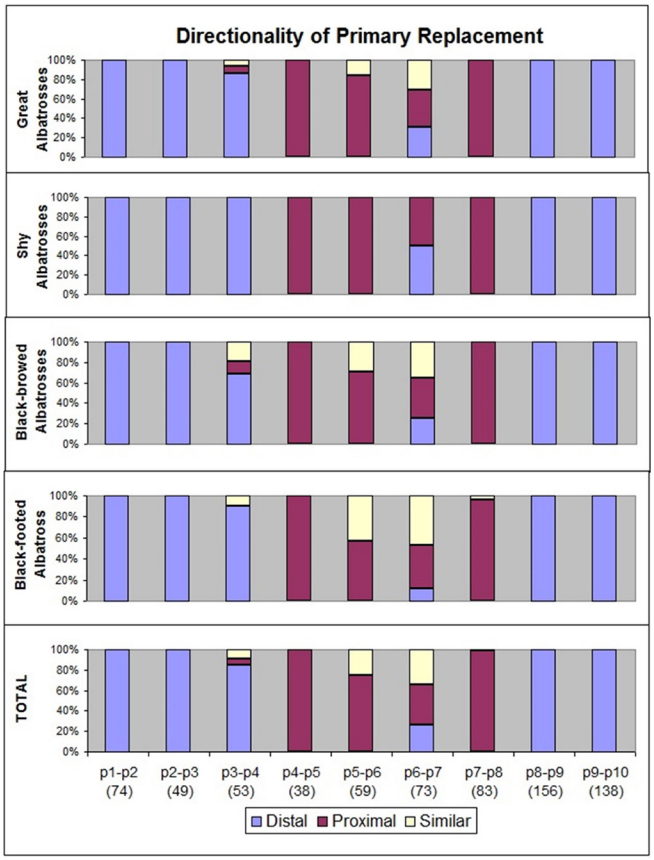

Fig. 3. The proportion of sequences (distal, proximal, or similar) between each pair of primaries during replacement of juvenile feathers. Sample sizes for each pair are given along the x-axis.

The distal series from p1 and the proximal series from p5 converged upon p3 or p4, the last two juvenile primaries to be replaced in 51 of 53 cases in which sequence among these feathers could be determined (Fig. 3). The two exceptions were a Great Albatross (ML 104516771) and a Black-footed Albatross (Fig. 4b), both of which retained juvenile p2 but had replaced the juvenile p4. Among the 30 cases in which the terminal feather replaced could be determined, p3 was the last feather replaced in 22 cases: five Great Albatrosses (e.g., Fig. 4c), two Shy Albatrosses, 10 Black-browed Albatrosses, and five Black-footed Albatrosses. The last feather replaced was p4 in three cases: one Great Albatross (ML609152689) and two Black-browed Albatrosses (ML576897371 and ML631250735). Replacement of p3 and p4 was judged to have occurred at about the same time in five cases: one Great Albatross (ML181845221) and four Black-browed Albatrosses (ML313396891, ML437019481, ML611299504, and ML631250735).

Replacement of Secondaries

Patterns of secondary molt were less diagnosable in the selected images because secondaries were smaller and often less visible than primaries. Noted replacement sequences were consistent with published accounts, proceeding distally from the tertials and proximally from s1, with the last secondaries replaced occurring among s7 to s17 (see examples in Fig. 4). A node at s5 was clearly present in three Black-footed Albatrosses (ML178709861, ML190124941, ML353894651), in which s1 and s5 were growing or new and s3–s4 remained juvenile. Two Black-browed Albatrosses showed replacement of s1 (ML627767896) or s1–s2 (ML631130126), but s3 inward (including s5) were juvenile. Five albatrosses showed replacement of s1–s5, with s6 inward remaining juvenile (Great Albatrosses ML282429281, ML419492111; and Black-browed Albatrosses ML611299504, ML627651427, and ML631012985). However, no albatrosses showed replacement of s3–s4 while s5 remained juvenile. Generally, first replacement of secondaries appears restricted to the tertials and, in some cases, s1 or s1–s2, whereas replacement of wing coverts was restricted to lesser and median secondary coverts. By the second replacement, more secondaries were replaced in sequence (with at least some secondaries among s7–s17 typically remaining juvenile) and most to all secondary coverts were replaced.

Timing of Primary Molt

Months in which 60 albatrosses were recorded replacing juvenile primaries are shown in Figure 6. Among sampled birds, Great Albatrosses (n = 14) showed little seasonal pattern to the replacement of juvenile primaries, whereas Shy Albatrosses (n = 7) and Black-browed Albatrosses (n = 11) replaced juvenile primaries

in October–February, and Black-footed Albatrosses (n = 26) replaced juvenile primaries in May–September. For birds inferred to be undergoing the second prebasic molt, replacement occurred in November–February for Shy Albatrosses, December–February for Black-browed Albatrosses, and July–September for Black-footed Albatrosses. For birds undergoing the third or fourth prebasic molt, replacement occurred in August–May for Great Albatrosses, October–November for Shy Albatrosses, October–February for Black-browed Albatrosses, and May–September for Black-footed Albatrosses. Older birds undergoing definitive prebasic molt (n = 84) showed less consistent timing (Fig. 6b), although molt in Black-browed Albatrosses was confined to January–June and in Black-footed Albatross to March–October.

DISCUSSION

Molt Timing and Extents

My results indicate that primaries p8–p10 are rather invariably first replaced during the second prebasic molt in Black-footed Albatross, in accord with previous studies (Howell, 2012; Langston & Rohwer, 1995; Pyle, 2008; Rohwer & Edwards, 2005), whereas many, if not virtually all, Great Albatrosses first replace primaries p8–p10 during the third prebasic molt, as inferred by Prince et al. (1997) and reported by Howell (2012) and Howell and Zufelt (2019). However, within *Thalassarche*, evidence for the molt cycle in which p8–p10 are first replaced has

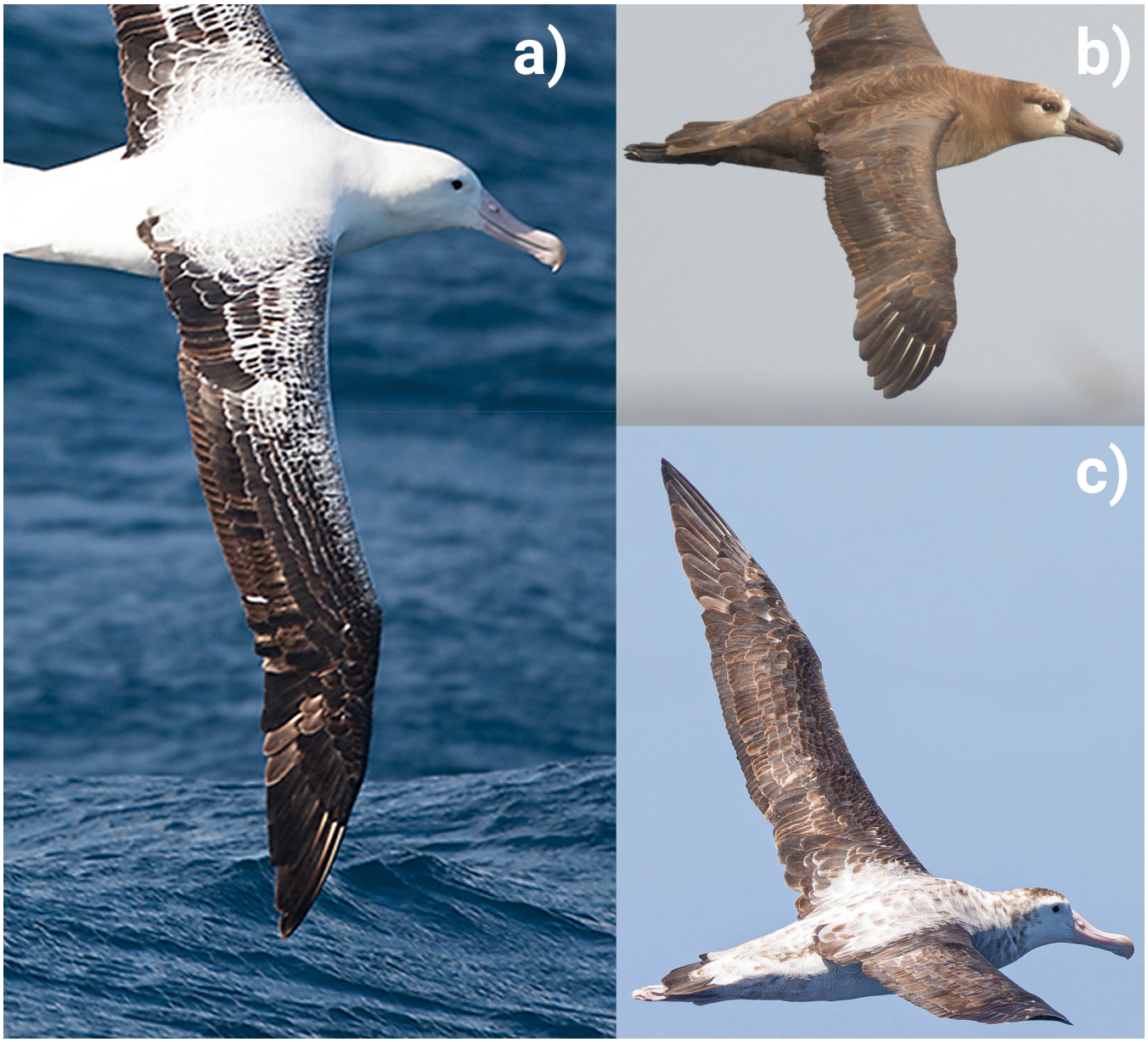

Fig. 4. Replacement sequences of the juvenile p2, p3, and p4 in albatrosses: (A) Great Albatross *Diomedea* sp. with the juvenile p3 and p4 retained, 01 Dec 2012 (see also text regarding secondaries and secondary coverts, and ML104516771, ML514798411, ML547275471, and ML614787282 for these patterns in other taxa); (B) Black-footed Albatross *Phoebastria nigripes* with the juvenile p2 and p3 retained, 07 Sep 2023 (see also ML65202531 and ML446366881); (C) Great Albatross *Diomedea* sp. with the p3 retained and the last feather replaced, 03 Dec 2023 (see also ML615074130, ML96591051, ML279616241, ML603678051, and ML431070911). Note also the blocks of juvenile secondaries remaining among s7–s17. Photo credits: © Tony Palliser (A, ML65202531), Max Wilson (B, ML614787282), and Kevin Bartram (C, ML612055977)

been questioned in some cases (e.g., Flood & Ryan, 2018) and may be based on circular reasoning around individual variation in molt patterns and maturation rates of plumage and bill coloration. For example, progressions of plumage and bill coloration with age may be less variable than previously supposed if age has been inferred primarily from the assumption that the replacement of p8–p10 only occurs during the third prebasic molt.

However, I inferred that two of 34 Great Albatrosses (5.8%), three of 15 Shy Albatrosses (20.0%), and seven of 27 Black-browed Albatrosses (25.9%) may have replaced primaries p8–p10 during the second prebasic molt (*cf*. Fig. 1). These birds showed plumage and bill characteristics that have been equated with the first or second cycle by several authors (Flood, 2014; Flood et al., 2015; Flood & Ryan, 2018; Howell, 2012; Howell & Zufelt, 2019; Jiguet, 2000), as well as fresher-than-expected juvenile primaries during the third molt cycle, largely retained secondaries, and secondary covert replacement confined to median and lesser coverts. These criteria have been equated more with the second rather than the third molt cycle in albatrosses (Howell, 2010, 2012; Prince et al., 1993, 1997; Pyle, 2008; Ryan & Adekola, 2023). Thus, our understanding of either the molt cycle in which p8–p10 are replaced or the maturation rates of bill and plumage coloration may need to be revised. Variation in the extent of



Fig. 5. Examples of albatrosses undergoing third prebasic molt with p7 and p6 being replaced in proximal, similar, and distal sequence: (A) Great Albatross *Diomedea* sp. with p7 dropped and p6 dropping on the left wing, indicating proximal replacement, whereas both p6 and p7 dropped simultaneously on the right wing, 22 May 2022 (see also ML60512201, ML331087781, and ML447825131 for simultaneous or similar replacement in this group); (B) Black-browed Albatross *Thalassarche* sp. with p7 growing and p6 juvenile indicating proximal replacement, 07 Dec 2024 (see also ML276705071, ML140893651, and ML190124941); (C) Black-footed Albatross *Phoebastria nigripes* with p6 longer than p7 indicating distal replacement (p8 is also being replaced for the second time), 16 May 2010 (see also ML615074130, ML392877821, ML299840181, and ML470622591). Photo credits: © Kevin Bartram (A, ML455125781), Pablo Gutiérrez Maier (B, ML627268447), and Matt Brady (C, ML44530591)

primary replacement during the second prebasic molt, ranging from no replacement to replacement of some primaries, has been documented in other large birds, including condors, pelicans, and large owls (Pyle, 2008), and may likewise occur in albatrosses. As such, the precise ageing of albatrosses based on molt phase may also need rethinking. It should be emphasized, however, that replacement of the juvenile p8–p10 during the second, third, or perhaps occasionally the fourth prebasic molt in southern albatrosses requires confirmation from ringed, known-age birds, which are currently unavailable because birds in these molt cycles remain largely at sea.

The timing of first replacement of p8–p10 in southern albatrosses also appears to vary and warrants further study. Howell (2012) provisionally indicates that, for the Black-browed Albatross, the second prebasic molt occurs from January–April, at 8–11 months since fledging, whereas the third prebasic molt occurs from April–September, at 20–23 months since fledging. The timing of these molts in Shy Albatrosses may vary with taxon and is poorly known (Howell, 2012). In the Wandering Albatross group, the second prebasic molt reportedly occurs from approximately December–September at 11–20 months since fledging, and the third prebasic molt occurs from April–October at 27–33 months since fledging (Howell, 2012).

In contrast, the findings of this study suggest that in Black-browed and Shy Albatrosses, replacement of p8–p10 during the second, third, and/or fourth/fifth prebasic molts can occur in October–February (Fig. 6a; *cf.* ML576897371, ML75539301, ML60512201, and ML457378951 for Black-browed Albatross and ML140893651, ML629057219, ML136412531, ML614473046 for Shy Albatross). These samples sizes are small and may be subject to bias relative to the distribution and timing of eBird contributions. Nonetheless, the combined results of these studies indicate a protracted period for each molt, during which p8–p10 might be replaced late during the second prebasic molting period or early during the third prebasic molting period.

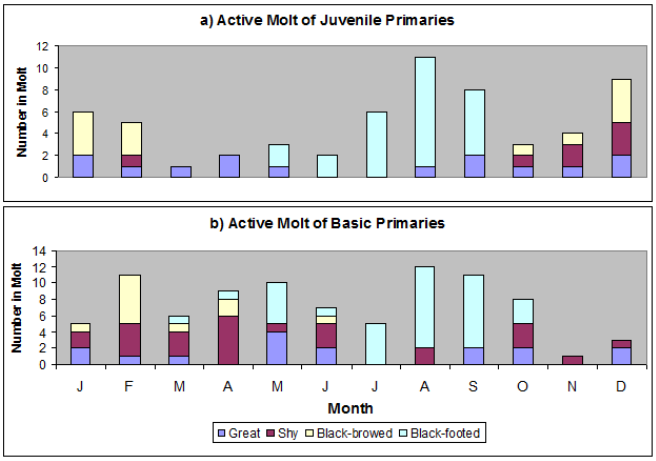

Fig. 6. Months (January–December) in which primaries were recorded actively being replaced in four taxonomic groups of albatrosses. (A) Replacement of juvenile primaries during second, third, and/or fourth/fifth prebasic molts; (B) replacement of basic primaries during definitive prebasic molts. See text for sample sizes and breakdown in month ranges for the second and third/fourth prebasic molts.

The timing reported for the definitive prebasic molt in the Black-browed and Shy Albatrosses, and for all molts of Great Albatrosses (Howell, 2012, p. 334), accords more closely with the results of this study, with molts occurring over protracted periods. The timing of predefinitive and definitive prebasic molts in Black-footed Albatross is also generally consistent with that of the literature (Howell, 2012; Pyle, 2008), with some exceptions. Great Albatrosses appear to have less seasonality in primary replacement, likely reflecting biennial breeding by most individuals; consequently, two traditionally defined molt cycles may occur between breeding seasons (Edwards, 2008; Howell, 2012; Prince et al., 1997).

Determination of Molt Cycles

Determining molt cycles in albatrosses according to the definition of Humphrey and Parkes (1959), as modified by Howell et al. (2003), is challenging due to several factors. The literature is inconsistent as to whether age is defined as time since hatching, as appears to be the case in at least some studies (M. Brooke, as cited in Flood, 2014, p. 98), whereas other studies do not specify precisely how age is defined (Jiguet, 2000; Prince et al., 1993, 1997). I agree with Howell (2010, 2012) that it is best to consider the first molt cycle as beginning at fledging rather than at hatching, because the first prebasic (prejuvenile) molt is often still underway at this time.

In the southern albatrosses and Short-tailed Albatross *Phoebastria albatrus*, which for the most part undergo biennial breeding, an initial molt of body feathers and, in some cases rectrices, can occur prior to first replacement of p8–p10 (Edwards, 2008; Howell, 2012; Prince et al., 1997; Pyle, 2008; Ryan & Adekola 2023; results of this study). Depending on interpretation, this molt has been inferred to represent either an inserted first-cycle (preformative) molt (Ryan & Adekola, 2023) or a partial second prebasic molt that does not include primaries (Howell, 2012; Pyle, 2008). In the Waved Albatross *P. irrorata*, by contrast, prebasic molts appear to be uniquely complete and rapid in a majority of birds (Harris, 1973; Kirwan et al., 2024; Monk et al., in press). Because this species lacks age-specific plumage and bill-coloration characteristics, the prebasic molt during which the primaries are first replaced remains unknown. It is possible that the second prebasic molt is complete.

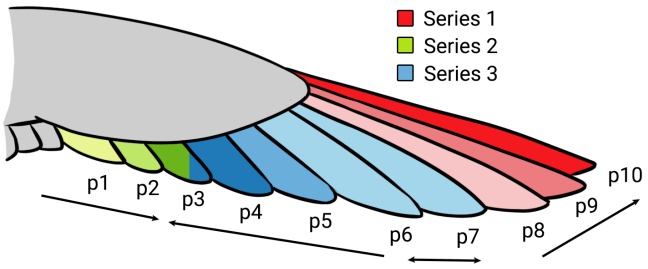

Fig. 7. Identification of three series of primary replacement in albatrosses based on the results of this analysis: p8 distally to p10, p1 distally to p3 or p4, and p6 or p7 proximally to p3 or p4; note that a commencement node appears to be fluid between p6 and p7. These sequences were consistent in all 14 taxa analyzed and appear to be consistent throughout the family Diomedeidae.

One possibility would be to define a molt cycle in biennial breeding albatrosses as spanning two years rather than one. Within a cycle, molt of body feathers and rectrices could precede replacement of p8–p10, followed by replacement of other primaries over a single two-year cycle. This interpretation would solve the issue of whether p8–p10 are first replaced at the second or third prebasic molt and also would account for the variable seasonal timing reported and noted above for the second, third, and fourth/fifth prebasic molts. However, a two-year molt cycle would be untenable if body feathers and/or rectrices are replaced twice within that period. Furthermore, molt in Black-footed and Laysan *P. immutabilis* Albatrosses appears to conform to an annual cycle, and the same may be true for birds of other biennially breeding species that return to breed the year following a failed breeding attempt (*cf*. Edwards, 2008; Prince et al., 1993, 1997). Therefore, for biennially breeding species, I consider it preferable to accommodate variation in replacement extent and timing within an annual molt cycle. In birds overall, timing, extent, and location of molts are highly variable within species, whereas sequence is substantially more fixed (Pyle, 2013). Additional data on replacement timing and extent among known-age birds in their first 1–3 years of life are needed to understand replacement timing and extent and to apply nomenclature to the first two to five prebasic molts of albatrosses.

Remigial Molt Sequences and Series

Based on replacement of juvenile primaries, I define three molt series (Fig. 7). A consistent series occurs from p8–p10, in all taxa, with no exceptions in sequence and extent. Reported variation in this series, e.g., just one or two of these feathers replaced, appears to be confined to molts of older (adult) albatrosses, which may be under increased time constraints for molting compared with pre-breeding aged birds. A second consistent series commences with p1 and proceeds distally to p3. I define a third series that can commence either from a node at p7 and proceed proximally to p4, or from a node at p6 and proceed bidirectionally to p7 and p4. I believe that this is the most parsimonious interpretation of replacement series in albatross and clarifies different interpretations in the literature regarding sequences among p1 to p7 and those between p7 and p8 (e.g., Howell, 2006; Langston & Rohwer, 1996; Rohwer & Edwards, 2006).

I have proposed that replacement nodes among primaries can be fluid along the alar tract within genera and even within species of parrots and falcons (Pyle, 2013), and I believe the same applies to albatrosses, with the third series commencing at either p6 or p7, or with both feathers synchronously. Occasional distal replacement of p6 to p7, with timing concurrent with the commencement of the distal sequence of p8–p10, e.g., during the third prebasic molt (*cf*. Fig. 5c), or during later molts involving Staffelmauser, can explain the interpretation of Langston and Rohwer (2005) and Rohwer and Edwards (2006) that the distal outer series commenced with p6 or with p7 (see also Howell, 2006). This underscores the importance of only considering replacement of juvenile feathers when defining complex molt series in birds. The results of this study also confirm a node at, and proximal replacement from, s5, although unlike in most diastataxic species (Pyle, 2008), all of s1–s5 can be replaced before s6 is replaced. This may have led to the supposition by some authors that a node at s5 was lacking.

Molt Strategies Among Albatrosses

Once modified remigial replacement sequences evolve along avian lineages, diverging from the common distal sequence within primaries and from nodes at the tertials, s1, and s5 in diastataxic species, they tend to remain consistent within families, indicating that molt sequences are evolutionarily conserved (Pyle, 2013). I predict that the three replacement series described here for albatross molt will be found in all species of Diomedeidae. Molt in Laysan and Black-footed Albatrosses is similar (Howell, 2012; Langston & Rohwer, 1995; Pyle, 2008; Rowher & Edwards, 2005), and examination of Macaulay Library images indicates similar patterns in the other two species of *Phoebastria*, Short-tailed Albatross (e.g., ML217211071, ML370037641, ML531456191) and Waved Albatross (e.g., ML613610240 ML613635116, ML627116004). Likewise, examinaion of Macaulay Library images indicates that molt follows the same replacement sequences and series in genus *Phoebetria* (e.g., ML24058811, ML248369491, ML615703500, ML621700894) and among taxa of *Thalassarche* other than Shy Albatrosses (e.g., ML282307211, ML414178781, ML560574331, ML583981571, ML609912348, ML616203577, ML629056342); see also Howell (2012) and Howell and Zufelt (2019).

Other elements of molt strategy, including timing, location, and extent, are less fixed in birds (Pyle, 2013). Among the taxa considered in this study, more additional primaries were replaced during the first replacement of p8–p10 in the smaller Black-footed Albatross than in the larger species, as expected given their shorter primaries and the lower energetic costs of replacing each feather (*cf*. Rohwer et al., 2009). Among the larger species, more additional feathers were replaced when p8–p10 were first replaced during the inferred third prebasic molt than during the inferred second prebasic molt, likely reflecting the additional foraging experience gained during the third year of life.

Another factor that appears to vary is replacement rates within each series. In this study, for example, p3 was the terminal feather replaced in the majority of Black-footed Albatrosses, whereas p4 was the terminal feather replaced in nearly half of the Great Albatrosses. I hypothesize that this difference may also relate to the smaller size and lower feather mass of p4–p6 in Black-footed Albatrosses compared with Great Albatrosses. Further investigation of variation in molt extent, timing, location, and replacement rates within series is needed to better understand the factors contributing to molt strategies in albatrosses.

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