PRIMARY MOLT IN THE BLACK-FOOTED ALBATROSS

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Molt is a critical part of every bird's life history, but there is a limit to the rate feathers can grow, which is about 4 to 10 mm/day in large birds (Prevost 1983). Hence some large and long-winged birds may have insufficient time between breeding seasons for a complete molt of their wing feathers, particularly the primaries (Langston and Rohwer 1996, Rohwer 1999). Molt of the primaries in most birds is sequential, from the innermost (primary 1, or p1) out to the outermost (usually p10), but some variations on this theme have developed in long-winged birds, so that they can fly more efficiently during molt. For example, the molt of albatrosses involves splitting the primaries into series. In the Black-browed (*Thalassarche melanophris*) and Gray-headed (*T. chrysostoma*) albatrosses, the outer three primaries are molted every other year, and some inner and middle primaries are molted every year (Prince et al. 1993). In the Black-footed (*Phoebastria nigripes*) and Laysan (*P. immutabilis*) albatrosses, the outer three primaries are usually molted every year, along with no to all inner and middle primaries (Langston and Rohwer 1995; pers. obs.). Year-to-year differences in the extent of primary molt reflect combinations of variation in the bird's age, breeding status, and food supply (Prince et al. 1993; Table 1).

Langston and Rohwer (1995) concluded that the primaries of Black-footed Albatrosses molt in two series: from a node at p6 outward to p10, and from a node at p5 inward to p1. In the outer series, p8–p10 are always replaced, but p7–p6 are not. In the inner series, from no to all primaries are replaced in a "wraparound" pattern; that is, a p5-inward-to-p1 sequence is maintained from one molt cycle to the next,

Table 1 Primary Molt of Eight Black-footed Albatrosses Captured 19–20 July 2005 at Cordell Bank National Marine Sanctuary, Marin County, California

Bird	p1	p2	p3	p4	p5	p6	p7	p8	p9	p10
704	O[a]	O	O	O	O	O	O	N[b]	90%[c]	65%
706	N	N	N	N	N	O	O	N	85%	30%
707[d]	O	O	O	O	O	O	O	O	95%	X[e]
708	N	N	N	N	N	N	N	N	75%	30%
709[d]	O	O	O	O	O	O	O	O	95%	45%
710	O	O	O	O	O	40%	45%	O	O	O
711	N	O	O	O	N	N	N	N	55%	25%
712	N	N	N	N	N	N	N	N	95%	25%

[a]O, feather one or two cycles old.

[b]N, feather newly replaced;

[c]Feather growing; percentage is a rough estimate of the fraction of the feather's full length beyond the primary-covert tips.

[d]Bird evidently in its second calendar year of life; molt being limited to p9 and p10 may reflect a year of poor food supply in the California Current (PRBO unpubl. data).

[e]X, feather shed or just starting to grow (not visible in photos).

so that replacement starts up again where it left off and the oldest feather is always replaced first. Subsequently, however, Edwards and Rohwer (2005) suggested that the inference of a wraparound pattern was an artifact of failing to recognize that the outer secondaries are part of a molt series that includes p1; they continued to treat the remaining primaries as split into series at a p5/p6 break.

From my observations of primary-molt patterns in albatrosses, I contend that the data used to support a p5/p6 break in the Black-footed Albatross are equivocal. I suggest, instead, that the molt sequence for the inner and middle primaries of all birds in table 6 of Langston and Rohwer (1995) can be interpreted as an inward stepwise molt that originates with p7. In stepwise molt, waves of molt move through a series of primaries, with successive waves starting before preceding waves have completed; thus the bird may be wearing at least three generations of primaries at one time. The stepwise molt I propose for the Black-footed Albatross differs from typical stepwise molt (which runs from p1 outward to p10) in starting with p7 and moving inward. Because p7 is the most exposed primary in the inner series, it can be replaced in preference to the innermost primaries, which experience relatively little wear and can be retained for two molt cycles (Table 2). I agree with Edwards and Rohwer (2005) that the wraparound molt is a spurious concept: figure 4 of Langston and Rohwer (1995) shows p1–p2 to be replaced more often than p3–p5, but in a wraparound pattern p5 should be replaced at least as often as the other primaries. P1–p2 being replaced more frequently than p3–p4 (figure 4 of Langston and Rohwer 1995) suggests a third (outward-molting) node at p1, or, as argued by Edwards and Rohwer (2005), perhaps p1 is aligned in a molt series with the outer secondaries. The Laysan Albatross (*P. immutabilis*) follows the same pattern that I report for the Black-footed (based on data in Langston and Rohwer 1995).

Langston and Rohwer (1995, table 6) had 11 actively molting specimens from which to infer directions of primary molt by the Black-footed Albatross, and none of

Table 2 Lengths of Primaries from Table 6 of Langston and Rohwer (1995) Expressed in Millimeters Rather Than as Percentages[a]

	p1	p2	p3	p4	p5	p6	p7	p8	p9	p10
Full length[b]	147	157	173	196	226	257	281	303	311	299
Bird										
12	O[c]	O	O	O	143	177	194	164	o[d]	o
145	O	O	O	O	38	57	28	o	o	o
171	O	O	152	172	206	218	194	30	o	o
16	O	O	138	157	192	231	28	o	o	o
25	O	O	166	188	224	252	o	o	o	o
289	O	55	154	174	203	o	183	61	o	o
98	1	93	138	157	217	O	219	88	o	o
154	29	N[e]	N	N	N	N	N	o	280	90
306	O	16	N	N	N	N	273	85	o	o
84	122	o	o	o	N	N	28	282	131	o
97	29	O	N	N	N	N	N	242	62	60

[a]All primaries grow at the same rate (Langston and Rohwer 1996), so longer feathers were shed before shorter feathers.

[b]Mean, from table 6 of Langston and Rohwer (1995)

[c]O, feather two cycles old.

[d]o, feather one cycle old (replaced in last molt).

[e]N, feather newly replaced.

these offers an unequivocal answer as to where the molt series break. I also examined spread-wing photos of eight Black-footed Albatrosses captured 19–20 July 2005 for satellite tagging (Table 1). These photos (birds 710 and 711 are shown on this issue's back cover) allow new, old, and growing primaries to be distinguished. But, as with data in table 6 of Langston and Rohwer (1995), interpretations of the molt pattern and series break in these photos can be equivocal. The lower photo on the back cover (of bird 711) exemplifies the difficulty of inferring molt sequences unless critical feathers are molting: it has p9–p10 completing growth, p8–p5 fresher-looking and blackish, thus newly replaced (but somewhat disheveled at the tips from handling), p4–p2 more faded and brownish, thus retained (probably one cycle old), and p1 newer-looking than p2–p4, perhaps newly replaced or perhaps one cycle old. I interpret this as an arrested inward wave from p7 and a complete outward wave from p8; whether p1 was molted as part of a different series cannot be determined. But molt in this individual could also be interpreted (following Langston and Rohwer 1995) as a complete outward wave from p6 to p10 and an incomplete wraparound molt within p1–p5. I also checked specimens (see acknowledgments) in search of birds molting these critical feathers, but only one bird (San Diego Natural History Museum 38861) was potentially informative: it was starting primary molt on 16 June, with p7 recently having been shed and the other primaries yet to molt. My data, together with a review of Langston and Rohwer's (1995) data (in the following paragraph), suggest that the molt break occurs between p7 and p8 rather than between p5 and p6.

Bird 12 (of Langston and Rohwer 1995, *see* Table 2) has an inward wave starting at p7 and an outward wave starting at p8. Bird 145 has an inward wave that started at p6 and a second inward wave starting at p7. Bird 171 has an inward wave that started at p6, a second inward wave starting at p7, and an outward wave starting at the recently shed p8. Bird 16 has an inward wave that started at p6 and a second inward wave starting at p7. Bird 25 has an inward wave that started at p6 (with p7 not yet shed). Bird 289 has an inward wave that started at p5, a second inward wave starting at p7, and an outward wave starting at p8. Bird 98 has inward waves that started at p7 and p5 and an outward wave starting at p8. Bird 154 has an inward wave that ran from p7 to p1 and an outward wave starting at p9 (p8 was skipped). Bird 306 has an inward wave starting at p7, a second inward wave that started at p6 has reached p2, and an outward wave is starting at p8. Bird 84 has an arrested inward wave that started at p6, a second inward wave starting at p7, a wave at p1, and an outward wave that started at p8. Bird 97 has an inward wave that started at p7, a wave at p1, and an outward wave starting at p8.

The upper photo on this issue's back cover shows a bird (number 710 in Table 1) whose molt is inconsistent with a break between p5 and p6: in this bird p8–p10 and p5–p1 are old, and p7–p6 are growing. Because p7 is longer than p6 it is logical to conclude that p7 was shed first. It is ambiguous whether p7 represents the start of an inward-molting wave (which I believe it does) or an outward-molting wave (with p6 starting the inward wave). Either way, the molt series are not split between p5 and p6.

From the above, I infer that p5–p7 typically molt inward from p7 and that p6–p7 are not part of an outer series. My observations support Langston and Rohwer's (1995) data for the annual, outward molt of p8–p10 by almost all birds (a few individuals, perhaps mainly first-year birds, replace only p9–p10; Table 1). If only p8–p10 are replaced, then molt is outward from p8 to p10; if inner and middle primaries are also replaced, then molt often starts at p7 and moves inward, sometimes as far as p3, before p8 is shed as the start of an outward wave; p9–p10 are often shed in close succession and grow simultaneously (e.g., lower photo on this issue's back cover). Further study of birds in molt is needed before molt series in the primaries of the Black-footed Albatross can be identified unambiguously, but observers now have an alternative hypothesis to consider.

Interestingly, a break between p7 and p8 corresponds to the pattern reported for the Black-browed and Gray-headed albatrosses, in which p8–p10 are molted outward every other year, and a second wave molts inward from p7 (Prince et al. 1993); a third (outward-molting) wave can also start at p1 in at least the Black-browed and Wandering (*Diomedea exulans*) albatrosses (Prince et al. 1993, 1997). Because molt sequences of the primaries are fairly conservative (P. Pyle pers. comm.), it would not be surprising if the Black-footed and Laysan albatrosses shared a common molt strategy with the southern albatrosses.

The frequency of molt of the outer primaries in albatrosses may reflect environmental conditions. In *Phoebastria*, abrasion by sand on the nesting islands and the effects of strong tropical sunlight may necessitate annual replacement of the outer primaries (whose tips are exposed on the closed wing), which is facilitated by molt occurring during fall in the productive California Current. By contrast, the high-latitude lifestyles of *Thalassarche* do not bring these species into contact with intense sunlight, and their primaries molt during midwinter, a potentially less favorable time (Prince et al. 1993); hence, they are able to replace the outer primaries only every other year.

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LITERATURE CITED

Edwards, A. E., and Rohwer, S. 2005. Large-scale patterns of molt activation in the flight feathers of two albatross species. Condor 107:835–848.

Langston, N. E., and Rohwer, S. 1995. Unusual patterns of incomplete primary molt in Laysan and Black-footed Albatrosses. Condor 97:1–19.

Langston, N. E., and Rohwer, S. 1996. Molt–breeding tradeoffs in albatrosses: Life history implications for big birds. Oikos 76:498–510.

Prevost, Y. 1983. The moult of the Osprey *Pandion haliaetus*. Ardea 71:199–209.

Prince, P. A., Rodwell, S., Jones, M., and Rothery, P. 1993. Moult in Black-browed and Grey-headed Albatrosses *Diomedea melanophris* and *D. chrysostoma*. Ibis 135:121–131.

Prince, P. A., Weimerskirch, H., Huin, N, and Rodwell, S. 1997. Molt, maturation of plumage, and ageing in the Wandering Albatross. Condor 99:58–72.

Rohwer, S. 1999. Time constraints and moult–breeding tradeoffs in large birds, in Proceedings of the 22nd International Ornithological Congress (N. J. Adams and R. H. Slotow, eds.), pp. 568–581. Birdlife South Africa, Durban.