MOLT IN LEACH'S AND ASHY STORM-PETRELS

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Broadly speaking, a bird's major energy-demanding activities during the yearly cycle are reproduction, molt, and in migratory species, migration. In many species, these activities do not overlap, presumably because of energy demands they each place upon a bird. Of particular interest to us are some species in the family Hydrobatidae. Harris (1969) felt the extended period required for molt in certain tropical storm-petrels prevents them from engaging in less-than-annual nesting cycles even though they are present in an environment that allows such regimes in other sympatric marine bird species. If molt can have such a governing effect on the energy budgeting of hydrobatids, its processes in this group should be of interest. Molt is relatively well known for only 6 storm-petrels—British, *Hydrobates pelagicus*: Scott (1970); Wilson's, *Oceanites oceanicus*: Roberts (1940), Beck (1970), Beck and Brown (1972); Harcourt's, *Oceanodroma castro*: Allen (1962), Harris (1969); Leach's, *Oceanodroma leucorhoa*: Harris (1974); Galapagos, *Oceanodroma tethys*: Harris (1969); and White-faced, *Pelagodroma marina*: Mayaud (1950), Browne *in* Palmer (1962)—but this information, with the exception of that for *H. pelagicus*, is confined largely to defining the extent of overlap among molt, nesting, and migration or post-breeding dispersal.

In an earlier paper (Ainley et al. 1974), we compared the life-histories of 2 species, the Leach's and the Ashy Storm-petrel (*O. homochroa*), that breed on the Farallon Islands, California. These 2 morphologically similar species were found to be similar in a few but different in most aspects of their life histories. In brief, Leach's Storm-petrels visit the Farallones for 7 months from late February to early September, and winter during intervening months in the tropical and subtropical waters of the eastern Central and North Pacific. They lay eggs during a 5½ week period from early May to mid-June. Ashy Storm-petrels visit the island for most of the year and usually remain within several hours flight of the island during all seasons. They lay eggs from late April to mid-July and sometimes later. We previously made some comparisons on molt (Ainley et al. 1974), explaining that it overlapped the pre-egg and chick stages of the annual cycle much more in the sedentary Ashy than in the migratory Leach's. In the present paper we present the full analysis of our work on the timing, sequences, and rates of molt in these 2 species.

METHODS

South Farallon, a rocky granitic island of 44 ha, is on the edge of the continental shelf at 37.4°N, 123.0°W, 43 km west of San Francisco, California. It and its neighboring islets

harbor the largest breeding concentration of marine birds in the U.S., excluding Alaska and Hawaii. The 1600 breeding Leach's and 4000 breeding Ashy Storm-petrels largely confine themselves to the southern quarter of the island (Ainley and Lewis 1974). Both species nest in greatest concentration under rocks on the south-facing talus slope of Lighthouse Hill (elevation, 109m).

We caught storm-petrels at night, when they were active about the island, by playing tape-recorded calls of Leach's to attract both species to mist-nets placed on the talus slope. We divided the calendar year into 73 five-day periods and attempted to capture at least 30 birds of each species in every period. The data reported here were gathered from 321 Leach's and 981 Ashy Storm-petrels trapped whenever weather permitted between April 1972 and April 1973. After each capture session, we banded the birds and recorded observations and measurements. The birds were then released while it was still dark, within 2 hours of capture.

We recorded molt, weight, wing length, color, and stage of incubation patch development. One of us recorded while the other measured. Molt was scored using the system devised and computer programmed for shorebirds by G. W. Page of the Point Reyes Bird Observatory. For each of 6 body regions, the number of growing feathers was scored on a scale of 0 to 3. The body regions inspected were: head, throat, flanks, belly, back, and rump. The 0 score indicated no molting feathers in a region, 0.5 indicated 1–3 growing, 1 indicated several, 2 indicated about every fourth feather growing, and 3 indicated most feathers growing. This last score, although found often in shorebirds and songbirds, was rarely encountered in storm-petrels. Molt in tail and wing feathers was scored differently. The 12 rectrices were numbered outward 1–6 from the center of the tail; primaries were numbered from the carpal joint outward, 1–10 (the eleventh vestigial primary was ignored); and the secondaries were numbered inward from the carpal joint, 1–14. We looked at all flight feathers of one wing and all tail feathers. Each was characterized as old, missing, 1/10, 3/10, 5/10, 7/10, or 9/10 grown, new, or of unknown age. We used these scores to determine rates and sequences but not the timing and intensity of molt. The latter was determined by totaling body molt scores and the number of growing tail and wing feathers for each bird, and by determining the mean, range, and 95% confidence limits for the number of growing feathers of all birds captured in each period. Five-day periods were combined into 10-day periods to increase sample sizes. We compared resultant values to the time of year and to the stage of nesting. After the period from 6 to 15 April, all birds with a downy ventral apterium were defined as immature and were analyzed separately. The ages of these birds were not known but some birds were one year of age (Ainley et al. 1974).

We compared intensity of molt to the stage of nesting in those Ashy Storm-petrels whose nests were under observation (Table 3). We confined these observations to parents that on occasion remained during the day in the late chick period (chicks 46–83 days of age), rather than taking from burrows birds that were incubating eggs or brooding small chicks. In this way we minimized nest desertions due to our activities. No nests of Leach's Storm-petrels were accessible. The state of the incubation patch was useful in correlating stage of molt to the nesting cycle (see Ainley et al. 1974).

THE TIMING AND INTENSITY OF MOLT IN ADULTS

Body molt.—The molt began for both species with a renewal of body feathers. We first found body feathers in the nests of individual Ashy Storm-petrels at the time their eggs were hatching, sometimes a little before and sometimes

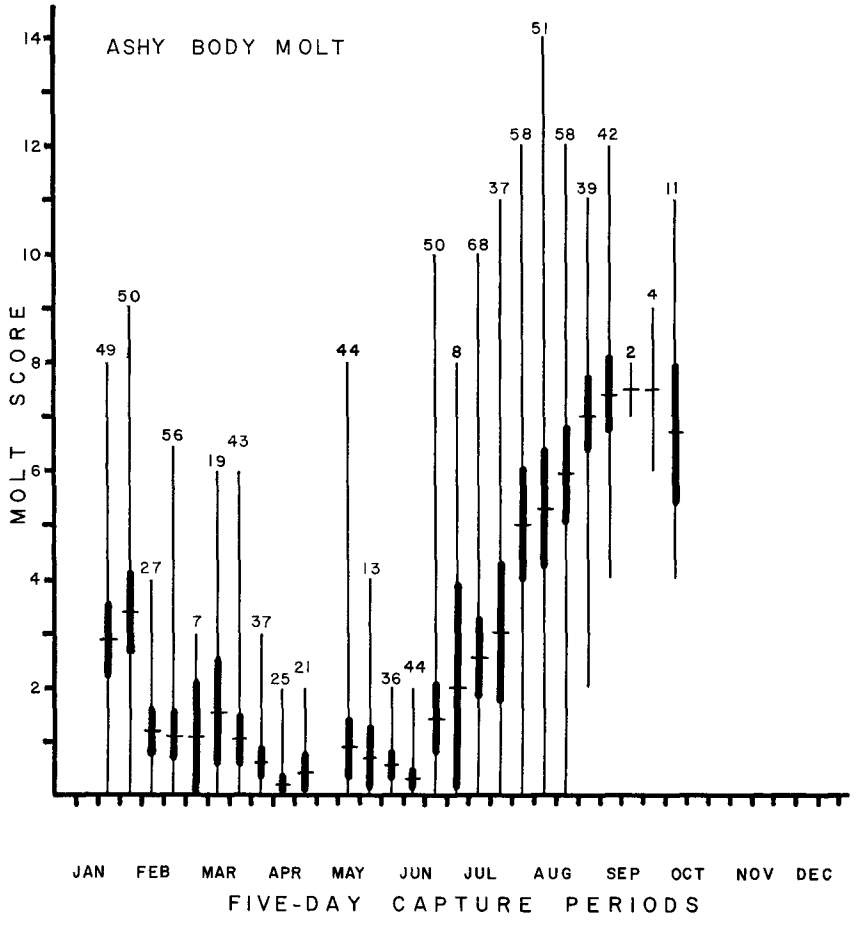

FIG. 1. The timing and intensity of body molt in adult Ashy Storm-petrels. Molt in the population during each 10-day period (combined 5-day periods) is described by the mean score, range, 95% confidence interval, and sample size.

a little after. Harris (1974) found the same in Leach's Storm-petrels nesting farther north in California. Leach's at the Farallones begin egg-laying a few days later than the Ashy, but their incubation period is a few days shorter. Thus for both species the first eggs hatch at the same time in the year (Ainley et al. 1974). In our netting sample, molting Ashy Storm-petrels first appeared between 15 and 19 June, and molting Leach's first appeared between 10 and 14 June (Figs. 1 and 2, Table 1).

Peak body molt scores in the Ashy were 12–14 and the highest mean scores

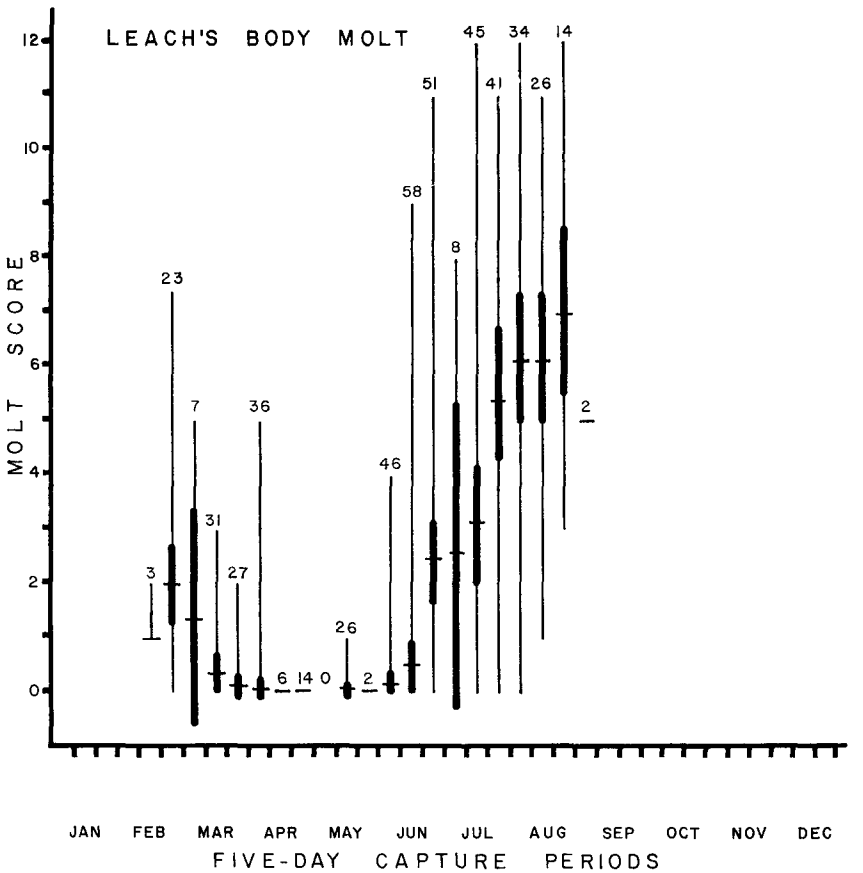

FIG. 2. The timing and intensity of body molt in adult Leach's Storm-petrels.

ranged from 7.0 ± 0.6 to 7.5 ±0.6 (Fig. 1, Table 1). Peak scores first occurred in the period from 4 to 13 August, about 50 days after body molt began. In an equal interval from the start of molt (ca. 40 days) both species reached a mean score of 7.04. We could not determine for sure if Leach's reached higher scores because we caught very few after the period when they reached the score of 7.04. The few we caught afterwards had lower scores and in the entire sample their peak scores ranged only 11–12, a lower range than in the Ashy. These facts and the fact that Leach's Storm-petrels require more time to complete body molt (see below) suggests a less intense body molt than in Ashy Storm-petrels.

Body molt continued coincidentally with molt in other feather groups. It

TABLE 1

A COMPARISON OF MOLT IN LEACH'S AND ASHY STORM-PETRELS

Comparison*	Species	Body	Tail	Primaries	Secondaries
1. Period Begun	L	32–33	36–37	46–47	52–53
	A	34–35	42–43	48–49	48–49
2. No. Periods from	L	–	4	10	6
Previous Molt Phase	A	–	8	6	0
3. No. Periods from	L	–	4	14	20
Start of Body Molt	A	–	8	14	14
4. Period of First	L	40–41	40–41	–	–
Peak Score	A	44–45	48–49	48–49	–
5. No. Periods, Start	L	8	4	–	–
to Peak	A	10	6	–	–
6. Four Highest Peak	L	11–12	8–9	4	–
Scores	A	12–14	7–9	6	12–14
7. Four Highest Mean	L	5.4–7.0	4.4–5.25	–	–
Scores	A	7.0–7.5	3.25–5.0	–	–
8. Days to Completion;	L	248–285	ca. 75	< 228	–
Mean		274	–	–	–
N (birds)		9	–	1	–
	A	228–283	–	166–181	124–160
		257	–	–	–
		12	–	4	4

* Data in comparisons 1, 4, 6, and 7 come from Figs. 1–7; in 8 from birds captured in molt during both the fall and spring (see Table 2); and in 2, 3, and 5 from other comparisons in this table.

was last to finish in the spring and did so about a week after the finish of molt in primaries and secondaries. It required slightly more time for completion in Leach's than in Ashy Storm-petrels ($P < 0.05$, t-test). In a sample of 9 Leach's caught both at the start of molt in the fall and its finish in the spring, the total time for completion ranged from 248 to 285 days (mean = 274 days, SD = 16). In a similar sample of 12 Ashies the elapsed time ranged from 228 to 283 days (mean = 257 days, SD = 17).

Tail molt.—Just before the start of true tail molt, rectrices were apparently lost easily, as indicated by birds having all tail feathers missing, or all on one side missing, etc. In this analysis, we considered tail molt to begin in the period immediately preceding that in which the first increase in mean tail molt score occurred. This was a few weeks after we first recorded adventitious molt. True rectrix molt began in Ashy Storm-petrels between 25 July and 3 August, about 40 days after the start of body molt (Fig. 3, Table 1), and coincided with or slightly preceded the attainment of peak intensity in the latter. This is also apparent in the case histories of recaptured birds (Table

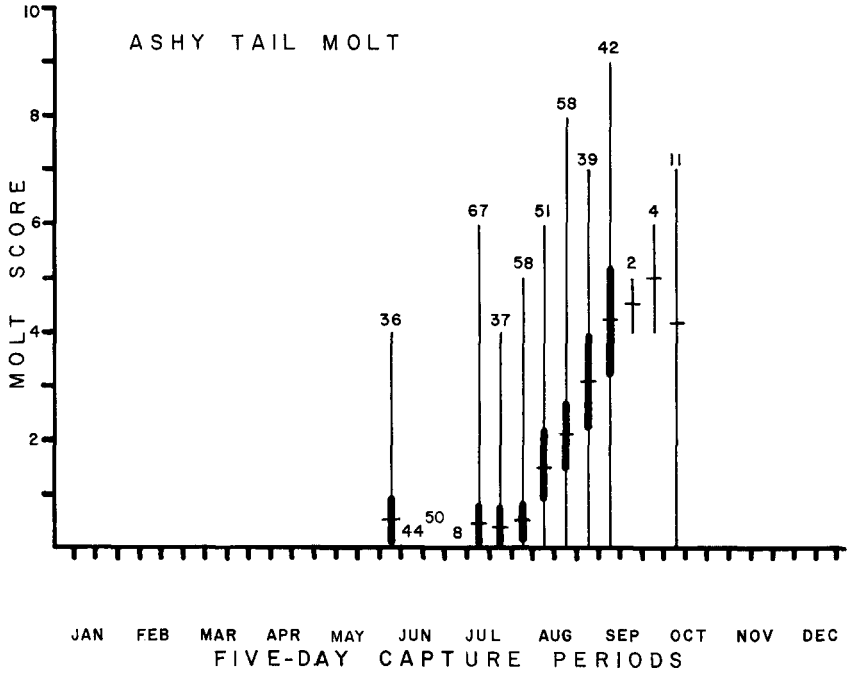

FIG. 3. The timing and intensity of tail molt in adult Ashy Storm-petrels.

2). Two Ashy parents with chicks 48 and 52 days old were the first found in tail molt, while one with a chick 46 days old had no tail molt (Table 3). That fits with what we observed in the netted birds. In contrast, Leach's began rectrix molt in the period from 25 June to 4 July, about 20 days after the start of body molt (Fig. 4, Table 1). Thus in this species, tail molt was begun earlier relative to the start of body molt and before attainment of peak body molt intensity.

In addition to beginning tail molt earlier, Leach's reached greater intensity of rectrix molt and did so much more quickly than Ashy Storm-petrels. Peak intensity of tail molt in the Ashy Storm-petrel was reached within 30 days after its start, but in the Leach's it was reached within 20 days. In the Ashy, high peak scores were 7–9 and high mean scores ranged from 3.25 ± 0.9 to 5.0 ± 1.0; whereas in the Leach's, high peak scores were 8–9 and high mean scores ranged from 4.4 ± 0.8 to 5.25 ± 0.7 (Table 1).

We have no direct measurements of the duration of tail molt, but apparently it required less time in Leach's than in Ashy Storm-petrels. This was suggested by the above information and by comparison of molt sequences (see below).

TABLE 2

MOLT SCORES OF BIRDS RECAPTURED SEVERAL TIMES

	Date	Primary	Secondary	Tail	Body
		Oceanodroma leucorhoa			
(1)	30 June	0	0	0	4
	15 July	0	0	5	4
	3 Aug	0	0	8	7
	20 Mar	0	0	0	0
		Oceanodroma homochroa			
(1)	9 Aug	0	0	0	8
	15 Aug	0	0	0	8
	26 Aug	0	0	1	7
	9 Sept	4	0	1	4
	6 Apr	0	0	0	2
(2)	3 Aug	0	0	0	7
	26 Aug	0	0	0	7
	9 Sept	0	0	1	10
	18 Oct	4	0	6	6
	6 Feb	6	14	0	4
	6 Mar	2	6	0	2
(3)	30 June	0	0	0	5
	15 July	0	0	3	10
	7 Aug	0	0	5	7
	30 Jan	2	2	0	3
	11 Feb	0	0	0	0
(4)	26 June	0	0	0	0
	19 Aug	0	0	0	4
	9 Sept	0	0	2	11
	16 Sept	0	0	3	6.5
	18 Oct	4	0	7	9
	2 Feb	6	12	0	7
(5)	25 May	0	0	0	1
	15 July	0	0	0	6
	7 Aug	0	0	0	12
	18 Sept	0	0	2	6
	17 Oct	4	0	5	6.5
	4 Feb	6	12	0	3
	18 Feb	4	0	0	1.5
(6)	26 June	0	0	0	3
	15 Aug	2 missing	0	6	7
	28 Aug	2	6	5	7
	3 Sept	2	6	4	7
	9 Sept	4	4	2	5
	2 Feb	2	4	0	2

TABLE 3

MOLT SCORES OF ASHY STORM-PETRELS HAVING CHICKS OF KNOWN AGE

Chick Age		Parent's Molt Score			
Days of Age	Days to Fledging	Primary	Secondary	Tail	Body
46	34	0	0	0	8
48	33	0	0	6	9
52	27	2	0	5	5.5
53	—	4	0	new	5
57	23	4	0	new	5
67	16	4	0	4	7
73	6	0	0	4	5.5
75	2	6	2	4	6
78	0	4	0	8	11
79	1	0	0	2	9
83	0	6	0	4	10

Our best guess, based on comparisons of growth rates for individual feathers and molt sequences, was that for Leach's Storm-petrels tail molt was completed in about 75 days and for Ashy Storm-petrels in about 95 days. Tail molt in Leach's was almost fully completed before the start of wing molt (see below), and it was about ¾ completed when the chick fledged and the parent ceased to visit the island. In the Ashy Storm-petrel, it was usually about ½ completed at chick fledging.

Primary molt.—Our first records of molting primaries in Ashy Storm-petrels occurred during the period 24 August to 2 September, when peak intensity of tail molt was reached (Tables 1 and 2). In the nesting birds, primary molt first appeared in parents having chicks 52–80 days of age (Table 3). Thus in this species, primaries began to molt 55–70 days after the start of body molt and about 30 days after the start of tail molt, when the latter reached peak intensity. In the Leach's most birds had fledged their chick and ceased to visit the island before primary molt began. We thus have few data on primary molt in that species. First records for primary molt in Leach's Storm-petrels occurred in the period 14 to 23 August. As with the Ashy, this was about 70 days after the start of body molt; unlike the Ashy, this was well past attainment of peak intensity in rectrix molt.

Among netted birds, the peak score recorded for the Ashy was 6 and for the Leach's it was 4 (Table 1), meaning 3 and 2 growing primary feathers per wing, respectively. The same respective scores occurred in 12 Ashy and 7 Leach's Storm-petrels which we examined in the collection of the California Academy of Sciences. These birds had been collected at sea off California

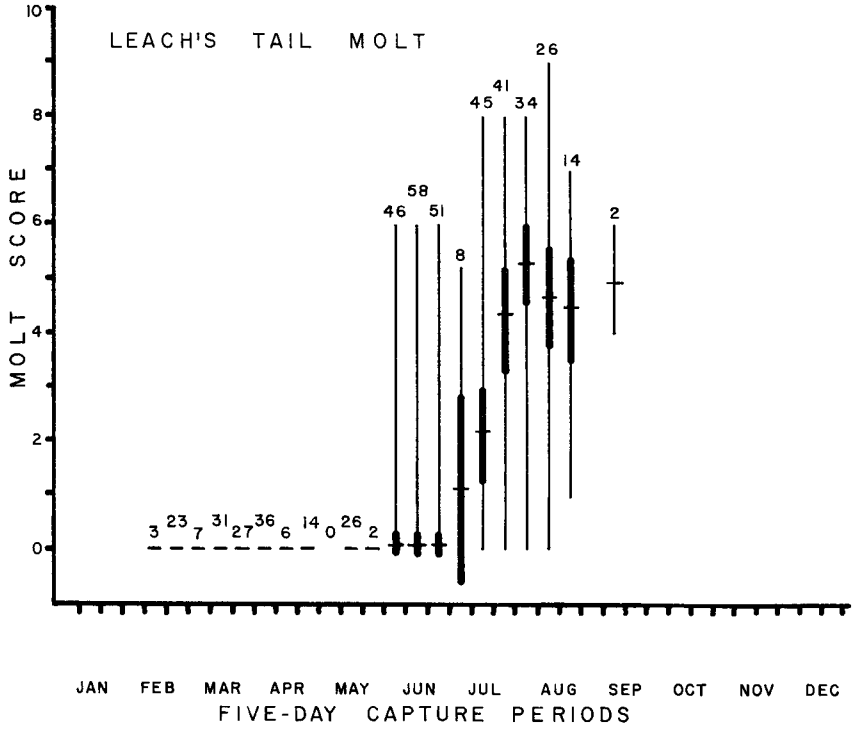

FIG. 4. The timing and intensity of tail molt in adult Leach's Storm-petrels.

during October and November of various years. Harris (1974) found only one Leach's Storm-petrel having 6 "molted" (= growing?) primaries in a sample of 53 molting birds. We recorded the peak score in the Ashy at the very start of primary molt during early fall, but we found the peak score in the Leach's (in the collected specimens) only during the late fall and early spring. Thus attainment of peak intensity of primary molt in Leach's Storm-petrel was delayed longer than in the Ashy, as well as being usually at a lower peak level.

Primary molt overlapped the period of visits during the pre-egg stage much more in the Ashy than in the Leach's Storm-petrel. Almost all Leach's (93% of 127 examined between 15 February and 15 April) had completed primary molt upon making their first spring visits to the island, and only 7% were still in the last stages of molt. In contrast, during the same period 25% of 189 Ashy Storm-petrels were in primary molt. This species, however, began visiting much earlier in the spring (Ainley et al. 1974), and of the 99 Ashy Storm-

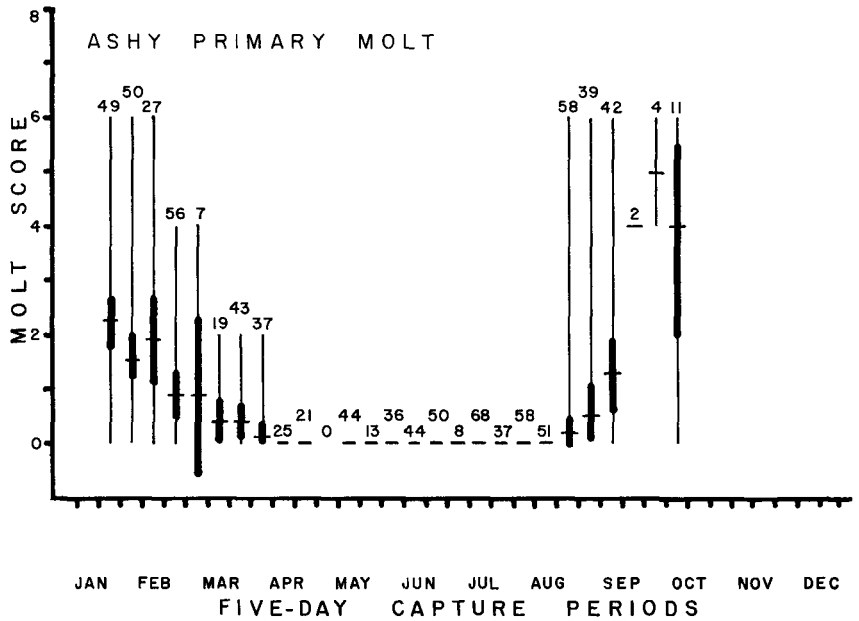

FIG. 5. The timing and intensity of primary molt in adult Ashy Storm-petrels.

petrels inspected between 26 January and 14 February, 68% were in primary molt. The last records of molt in primary feathers occurred for both species between 5 and 15 April (Figs. 5 and 6).

In a sample of 4 Ashy Storm-petrels caught in primary molt both during the fall and spring, the duration of molt ranged from 166 to 181 days. All that can be said here for Leach's Storm-petrels is that primary molt can last less than 228 days ($n = 1$ bird). Primary feather renewal may take a bit longer in the Leach's as indicated by the delay in attainment of peak intensity and the lower peak scores relative to those of the Ashy.

Secondary molt.—Ashy Storm-petrels began molting secondaries between 24 August and 2 September, coincident to the start of primary molt (Table 2, Fig. 7). In Leach's, on the other hand, secondary molt started at least 30 days after the start of primary molt (Table 1, Fig. 6). The first Leach's in secondary molt was caught in the period from 13 to 22 September.

Both species finished secondary molt coincidentally with the end of molt in primary feathers. Similarly to primary molt, then, the last birds of both species that were renewing secondaries were found between 6 and 15 April. In a sample of 4 Ashy Storm-petrels, the secondaries required 124 to 160 days for completion of molt, less time than required for primaries. The explanation

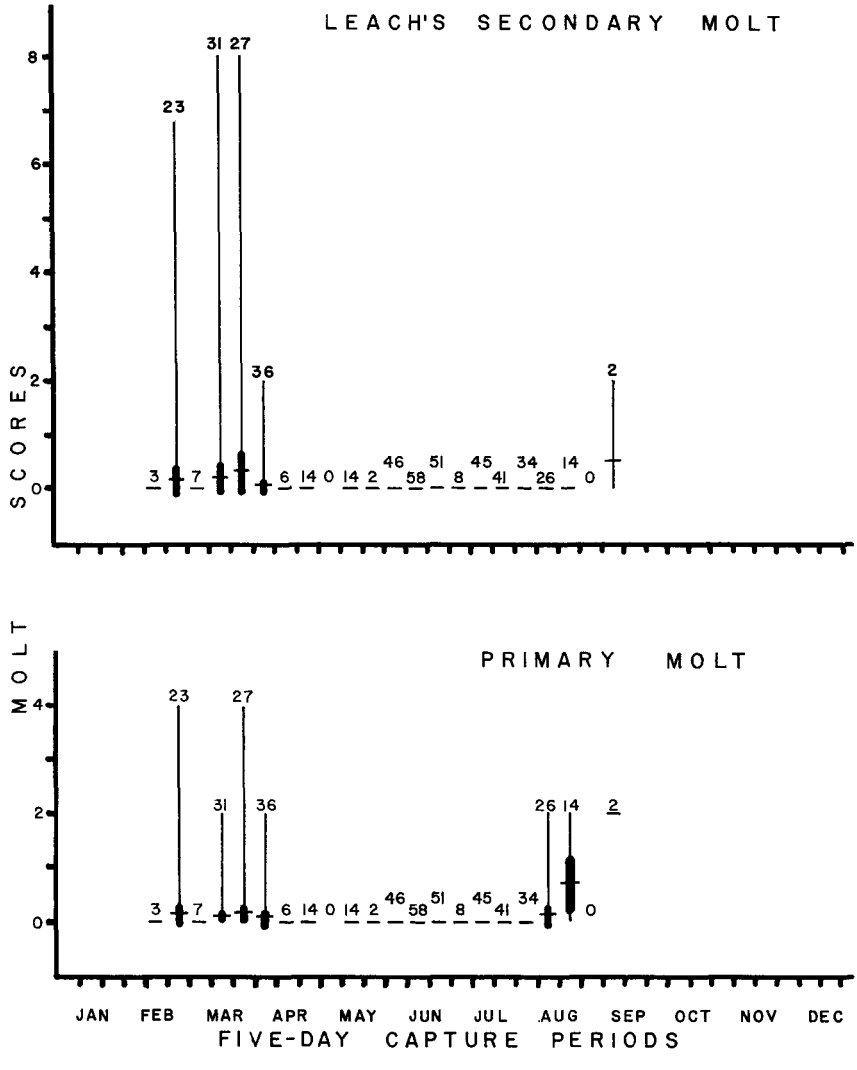

FIG. 6. The timing of primary and secondary molt in adult Leach's Storm-petrels.

for more rapid renewal of secondaries will become apparent in the section on molt sequences. We have no data on the duration of secondary molt in the Leach's but it must be shorter than in the Ashy because unlike in the latter, it began well after the start of primary molt yet ended at the same time. The peak secondary molt scores in the Ashy Storm-petrel were 12–14, or 6–7 grow-

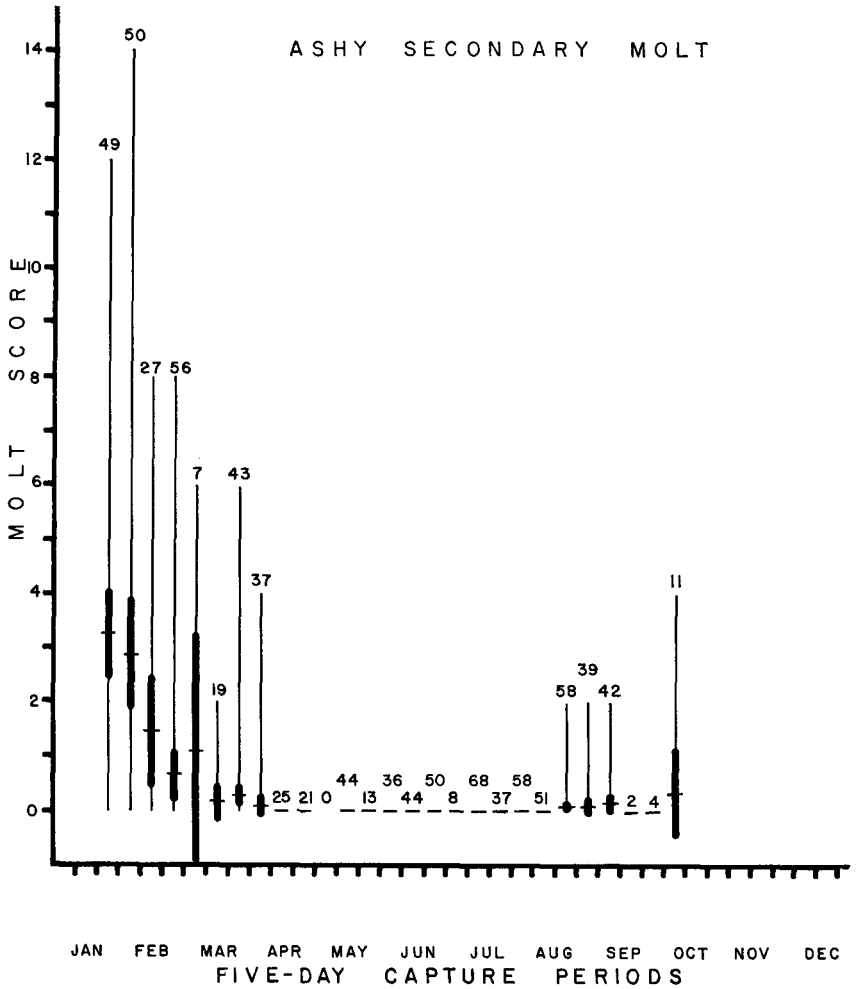

FIG. 7. The timing and intensity of secondary molt in adult Ashy Storm-petrels.

ing secondaries per wing; but all we can say for Leach's is that peak scores were somewhere above 8, or 4 growing secondaries per wing.

SEQUENCES OF MOLT

Body molt.—Little can be said about molt sequence in body feathers. The first body region in which molt began was usually the belly and the last to complete molt was usually the forward part of the head (the face).

Tail molt.—The sequences of feather loss and replacement were the same in both species, but a noticeable difference occurred in rate of sequence progression. In about a third of the birds checked, no clear pattern was discernible; but in the remainder the following sequence occurred with some variation. The most constant element of the sequence was that pair 5-5 (the next to outermost feathers on either side) was the last to be lost and the last to complete growth. This pair of feathers was dropped when the outermost pair (6-6) reached 7/10 to 9/10 growth. The outer pair was usually the first or second pair to be molted. This system insured use at all times of at least one pair of the longest, outermost feathers in the tail. The forked tail in these storm-petrels probably enhances balance and maneuverability in their characteristic darting and dipping flight.

Tail feathers were most commonly lost in the order: 6, 4, 2, 1, 3, 5 (Fig. 8). Thus every other feather on either side of the tail was lost in succession from the outside pair toward the center and then from the center toward the outside. The major difference between the species was that in Leach's Storm-petrels, feathers 1, 3, and 5 began their molt much sooner relative to growth in 6, 4, and 2. The result should be, and nothing suggested otherwise, that rectrix molt required less time for completion in the Leach's Storm-petrel. In fact because the shorter inner feathers required less time to complete growth (due to their shorter length, see below), the inner 4 feathers often completed growth before the 6-6 pair. It appeared in some individuals of Leach's that the 1-3-5 set began molt almost simultaneously to the 6-4-2 set. This was rarely the case in the Ashy.

The sequence just described differs from that in the British Storm-petrel, in which rectrices merely molt in pairs from the central ones outward (Scott 1970).

Primaries and secondaries.—The following sequence description was determined for Ashy Storm-petrels. Based on the 7 molting specimens of Leach's in the California Academy of Sciences, it is seemingly the same for that species also. The problem was that we caught Leach's Storm-petrels in the very beginning or the very end of primary molt but never in any intermediate stages of wing feather renewal. The major difference between the species appeared to be in rate of feather loss. Scott (1970) described about the same sequence in the British Storm-petrel.

Primaries 1 and 2 were dropped simultaneously. When these became ⅓ grown, primary 3 and secondary 12 were lost. Hereafter, once a primary became about ⅓ to ½ grown (with the previous one being ½ to ¾ grown) the next one was dropped. Secondaries 12 to 14 (the tertials) were lost very slowly and they also grew quite slowly, such that when primary 6 was dropped, secondary 12 was just about fully grown but 13 had not yet been lost. How-

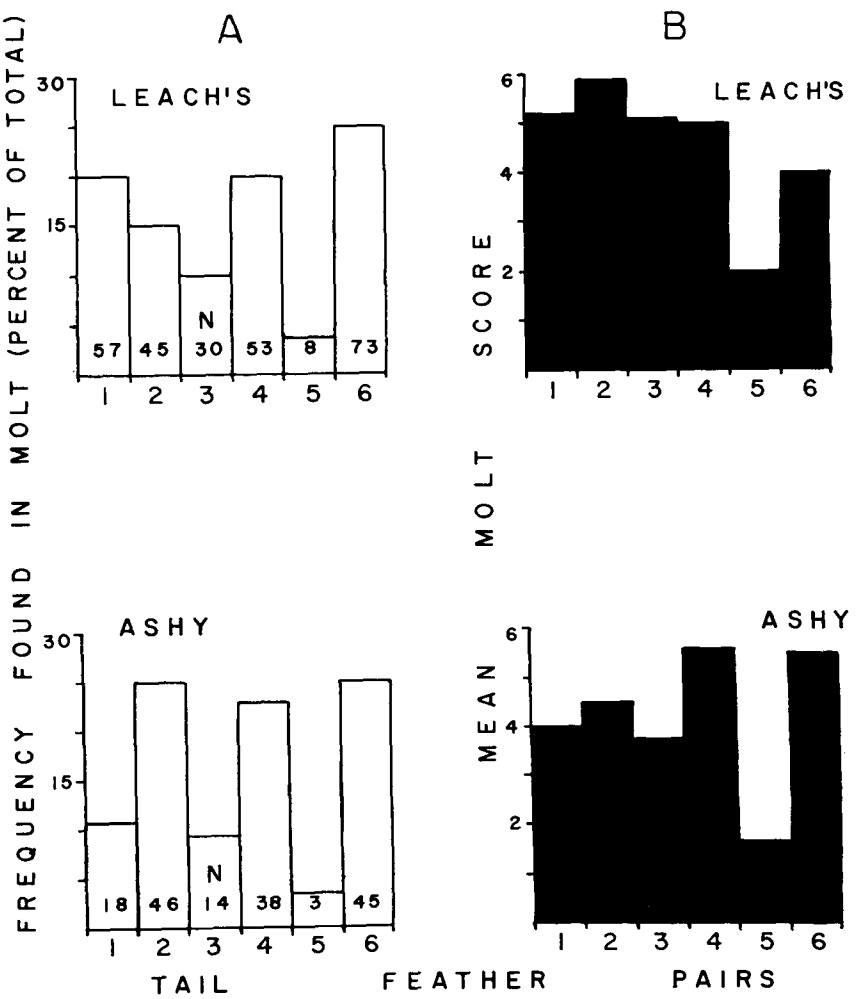

FIG. 8. The sequence of tail feather replacement in Leach's and Ashy storm-petrels, as shown by sample sizes (A) and molt scores (B) of feather pairs. The sequence of feather loss is evident in (A) assuming that feather pairs most often found in molt are first to start and pairs least often found in molt are last to start. Molt scores (B) indicate the rate of feather loss—one species relative to the other—by showing the extent of growth in each feather compared to others.

ever, when primaries 9 and 10 had reached full growth, secondaries 13 and 14 had completed their growth. When primary 7 was dropped so were secondaries 1 and 5. Secondary feather replacement then passed successively inward from these 2 centers. When primary 8 was lost so was secondary 11, and

TABLE 4

RATES OF FEATHER GROWTH IN BIRDS RECAPTURED DURING MOLT

Tail Feather	6	5	4	3	2	1
			Oceanodroma homochroa			
Score change/day	.023	.023	.028	.035	.037	.035
N	23	3	12	7	16	8
Total days	44	44	36	29	27	29
Feather length (mm)	84	79	70	64	60	58
mm/day growth	1.9	1.8	2.0	2.2	2.2	2.0
			Oceanodroma leucorhoa			
Score change/day	.023	.024	.027	.032	.036	.038
N	13	1	5	4	6	5
Total days	44	44	37	31	28	26
Primary Feather	10	9	4	3	2	1
			Oceanodroma homochroa			
Score change/day	.022	.013	.017	.023	.026	.026
N	3	1	1	3	6	6
Total days	45	77	60	43	39	39
Feather length (mm)	93	107	78	69	61	55
mm/day growth	2.0	1.4	1.6	1.6	1.5	1.4

feather replacement then passed successively outward from 11 to 9. The last feathers to complete growth, just about simultaneously, were primary 10 and secondaries 4 and 9. In summary, primary feather molt passed outward from one center (the carpal joint) but secondary feather molt proceeded from 4 centers: the carpal joint inward, secondary 5 inward, and secondary 11 and 12, inward and outward, respectively. The greater number of growing feathers allowed the secondary molt to be completed in a time less than or equal to that of the primaries.

RATES OF FEATHER GROWTH

Rectrices.—Rate of change in the molt score (i.e., extent of growth) increased from .02 score points per day for feathers 5 and 6 to .04 score points per day for feathers 1 and 2 (Table 4). Considering the different lengths of the feathers, rate of growth was actually about the same for all tail feathers, about 2 mm per day. Thus, the longer, outer feathers required more time to complete growth than the shorter, inner ones: feathers 5 and 6 required 44 days, feather 4 required 36 days, and feathers 1, 2, and 3 required 27 to 29 days. These observations were for Ashy Storm-petrels, but similar growth

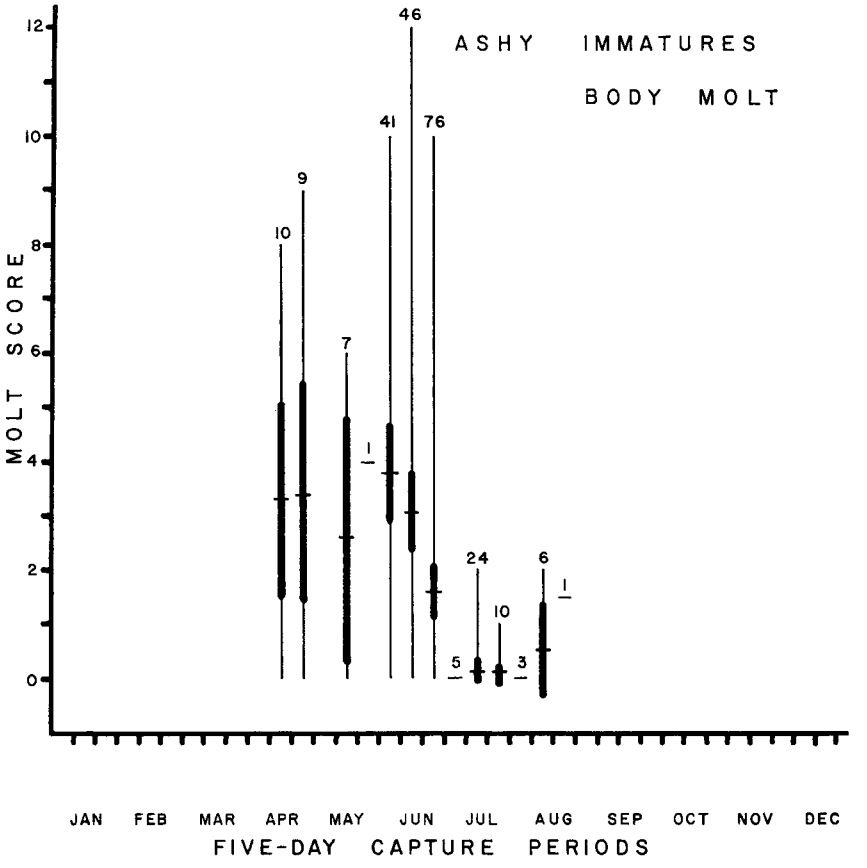

FIG. 9. The timing of body molt in immature Ashy Storm-petrels.

rates occurred in the tail feathers of Leach's Storm-petrels. It seems, therefore, that a faster rate of feather loss rather than faster growth accounts for the faster progression of rectrix molt in the Leach's compared to the Ashy.

Primaries.—Data were available only for determination of growth rates in the primaries of the Ashy Storm-petrel. The length of time required for completion of growth again depended on feather length. Changes in molt score in recaptured birds ranged from .03 points per day in the shortest, inner primaries to .01 in the longest, outer ones. Primary 9, the longest wing feather, required about 77 days to grow and primaries 1 and 2, the shortest, required about 39 days. The true growth rate of primaries was generally less than 2 mm per day, and thus was slower than in the rectrices.

MOLT IN IMMATURES

All birds of both species having no incubation patch (score of 0; Ainley et al. 1974) after period 20 (about 10 April) were considered immature. Probably some having a partially downy ventral apterium (score of 1) were also immature but we could not separate them from adults. These immatures probably accounted for the records of body molt in "adults" during the egg stage (see Figs. 1 and 2). In breeding adults, as shown earlier, body molt did not begin until about the time of egg-hatching.

Body molt began earlier in the year in immatures. We had a much larger sample of immature Ashy Storm-petrels with which to work (Fig. 9), but the few immature Leach's examined by us exhibited similar patterns. Most immature Leach's Storm-petrels apparently stopped visiting the island before beginning body molt, but most immature Ashy Storm-petrels visited while in body molt but ceased visiting prior to the start of tail molt. Immatures, however, made very few repeat visits (Ainley et al. 1974). We recorded heavy body molt in immature Ashy Storm-petrels during the period from 16 April to 4 July, the time of year to which their visits were restricted, and when little molt was recorded in adults. Assuming temporal patterns to be similar, immatures should also have begun molt in the tail and wings earlier in the year than adults.

Crossin (1974) discussed the incidence of molt in specimens of *O. l. leucorhoa* and *O. l. beali* (the Leach's subspecies breeding at the Farallones) collected at sea by the Pacific Ocean Biological Survey Program in the eastern Central and North Pacific Ocean. Assuming that molt regimes of both subspecies are similar relative to the breeding cycle, and considering that *O. l. leucorhoa* in Alaska lays eggs about a month later than *O. l. beali* at the Farallones (compare Bent 1922, with Ainley et al. 1974), then the individuals of both subspecies he found in primary molt during the spring were probably adults. The majority of collected specimens, and more so for *O. l. leucorhoa* than *O. l. beali*, however, had completed primary molt by November or December and sometimes by October. There seems little doubt that these birds, which apparently contributed large numbers to the Central Pacific populations, were non-breeders and probably immatures. Assuming that primary molt requires about 170 days for completion, the first adult *O. l. beali* found in primary molt at the Farallones should have finished this molt phase during the last week of January.

DISCUSSION

Comparison of the timing and intensity of molt and its various phases in the 2 storm-petrels reveals some interesting differences that agree with the general divergence in life styles outlined in a previous paper (see Ainley et

al. 1974). In general, these relate to differences in the time and energy budgeting of a short-ranging, sedentary species—the Ashy Storm-petrel—and a long-ranging, migratory species—the Leach's Storm-petrel. In the Ashy, molt overlaps extensively with reproduction and with a limited post-breeding dispersal. In particular, much overlap exists between wing feather molt and the chick and pre-egg stages of successive nesting cycles. In the Leach's molt places a minimum of demand on energy budgeting during the pre- and post-breeding migrations, and in even greater contrast to the Ashy, wing feather molt barely overlaps any phase of reproduction.

Scott (1970) compared the molt regimes in petrels, except the albatrosses, by grouping 18 species and subspecies on the basis of (1) breeding latitude (high, temperate, tropical), (2) type of post-breeding movement (transequatorial migration or dispersal into adjacent seas), and (3) molt regime (*a*, molt after the wintering area had been reached; *b*, molt started at the breeding grounds and completed quickly before dispersal; *c*, molt started after breeding but completed slowly to end just before the next breeding cycle; and *d*, like the last but molt started at the breeding grounds). The second of these regimes has yet to be reported for a hydrobatid. His breakdown by breeding latitude was deemed important to the study of molt and post-breeding movement based on the widely accepted generality that ocean productivity, and thus food availability and the potential for energy uptake, declines from high to low latitudes.

In the sub-Antarctic and in temperate latitudes, species such as *Oceanites oceanicus* (Roberts 1940, Beck 1970, Beck and Brown 1972) and *Pelagodroma marina* (Mayaud 1950, Browne *in* Palmer 1962) finish breeding and then fly quickly to the wintering area where molt occurs (regime *a*). Tropical species such as *Oceanodroma castro* (Allan 1962, Harris 1969) and *Oceanodroma tethys* (Harris 1969), which disperse into adjacent seas after breeding, require the entire period between annual breeding cycles to complete the molt (regime *c*). Finally, the temperate species *Hydrobates pelagicus*, which winters across the equator in south temperate seas, begins its molt late in nesting, and then like tropical species, requires the entire period until the next breeding cycle for its completion (regime *d*; Scott 1970).

Leach's Storm-petrels from the Farallones are most similar to the British Storm-petrel in their patterns of reproduction, molt, and migration. One possible relating factor is that the subtropical waters inhabited by the Leach's during their breeding season (see Ainley et al. 1974) are similar in productivity to waters of the eastern North Atlantic and Mediterranean areas (see Gulland 1971) inhabited by the British Storm-petrels during their breeding season. Both then leave nesting areas to migrate into or across tropical waters for the winter.

The pattern of reproduction, molt, and post-breeding movement exhibited by Ashy Storm-petrels does not fit into any of Scott's categories. No other hydrobatid so far studied overlaps molt, and especially that of flight feathers, so extensively with both the chick stage of one nesting cycle and the pre-egg stage of the one following. The Ashy Storm-petrel, based on the knowledge available, is the most sedentary species in its family. Individuals are absent from the Farallones for less than 2 months each year, but even during that time they are within several hours' flight of the islands. Throughout the year they inhabit the subarctic waters of the California Current. Their sedentary nature and extensive overlap between molt and nesting correspond logically to the high productivity and food availability of the waters they inhabit; the California Current off central California is among the most productive ocean regions in the world (Gulland 1971).

SUMMARY

Molt in Ashy Storm-petrels proceeds rather regularly from one phase to another; when one phase reaches peak intensity the next begins. In adults, body molt starts at about egg-hatching, 40 days later rectrices begin their molt, 30 days after that primaries begin molt, followed by secondaries almost immediately. Most Ashy Storm-petrels have half-completed tail molt and are molting the first 2 or 3 primaries when their chick fledges. They are still molting the last 2 or 3 primaries on their first visits to the island in the following nesting cycle. The total time required for molt averages 257 days.

Molt in Leach's Storm-petrels proceeds in the same order but the intervals between start of the various phases differ. Tail molt begins only 20 days after start of body molt, 50 days later primaries begin molt, and about 30 days after that molt in the secondaries begins. When the chick fledges, parents have almost completed tail molt but usually have not begun wing molt. Most Leach's Storm-petrels complete molt before visiting the island in the following breeding cycle. Total time required for molt averages 274 days.

The sequences of feather replacement and the rates of growth in individual feathers are described.

Immatures begin molt earlier in the year than adults, starting about the time the latter are laying and incubating eggs.

Little overlap occurs between molt and migration, and between primary molt and breeding in the Leach's compared to extensive overlap between these activities in the Ashy Storm-petrel. The different molt regimes correspond to the overall divergence in life styles of the 2 species, Leach's being a long-ranging, migratory species of subtropical open-ocean waters and the Ashy being a short-ranging, sedentary species inhabiting subarctic coastal waters. Molt in the Leach's is similar in its timing and degree of overlap with other activities to the British Storm-petrel; but the molt regime in the Ashy is unique among storm-petrels so far studied.

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