MOLT OF THE SPOTTED OWL

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ABSTRACT.—The molt of both wild and captive Spotted Owls was studied in Oregon between 1970 and 1980. Spotted Owls developed three plumages in their first year. The white natal down was replaced by the fluffy juvenal plumage before owlets left the nest. Replacement of the juvenal feathers by the basic I plumage began when owlets were 47–56 days old and was complete by late September or October. The only juvenal feathers not replaced during the latter molt were the remiges, rectrices, and greater primary coverts.

Adults underwent a prolonged prebasic molt each year between April and mid-October. The molt of the body feathers was complete annually, but 2 yr (rarely 3) were required to molt all of the remiges, rectrices, alulars, and greater wing coverts. The most common pattern of tail molt was a rapid or "simultaneous" molt, but irregular and partial molts also occurred. *Received 12 March 1980, accepted 5 May 1981.*

LITTLE is known about the molt of the Spotted Owl (*Strix occidentalis*). Bent (1938) and Miller (1974) presented incomplete descriptions of plumage development in young Spotted Owls but did not discuss later molts. Oberholser (1974) stated that adult Spotted Owls underwent a complete annual molt but he did not indicate how he determined that the molt was complete. Indeed, although some authors (e.g. Bent 1938, Dement'ev et al. 1951, Oberholser 1974) have assumed that the annual molt in *Strix* was complete, I have been unable to find any studies in which a complete molt was documented in this genus except for the Tawny Owl (*Strix aluco*) (Piechocki 1968a).

The pattern of tail molt in the Spotted Owl is also unclear. Mayr and Mayr (1954) suggested that the tail molt occurred gradually in all owls in the genus *Strix,* but Piechocki (1968a) found that Tawny Owls molted the rectrices rapidly or "simultaneously." Two Spotted Owls collected by Huey (1913) and one collected by Johnson and Russell (1962) had also molted their rectrices rapidly. Because so many statements in the literature concerning the molt in *Strix* are either unverified or incorrect, carefully documented studies on the molt in this group of owls are needed.

Between 1970 and 1980, I conducted a series of studies on the distribution, reproductive biology, and ecology of the Spotted Owl in Oregon (Forsman 1976, 1980). During these studies I observed many Spotted Owls in the field and raised two Spotted Owls in captivity. Records were kept of the molt of all owls observed. This report describes the molt of the Spotted Owl based on my observations of both wild and captive birds.

METHODS

Owls observed in the field included 339 adults and 95 fledglings. Most observations were conducted between March and September each year, when I made regular visits to Spotted Owl nests and roosts. During these visits, any recently molted feathers were collected from below roost trees, and the owls were examined at close range with binoculars for evidence of molt. Sixteen adults were examined when I trapped them to install radiotransmitters and when I retrapped them to remove the transmitters. Almost daily observations were made of eight of the radio-tagged owls between May 1975 and June 1976 and

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Fig. 1. Sequence of feather replacement during molt from juvenal plumage into basic I plumage. A. 42–46 days old, 10 days after leaving nest. B. 90–100 days old. C. 140–150 days old; note white tips of juvenal rectrices.

of six other radio-tagged individuals between April and September 1980. Six nestlings between the age of 5 and 25 days were examined to determine the pattern of molt in nestlings.

The two captive owls (both females) were confined in separate outdoor cages with wire mesh sides and corrugated metal roofs. Cage dimensions were 2.5 × 3.6 × 2.5 m and 2.5 × 3.0 × 2.1 m, respectively. One captive (1A) was obtained as a 3-week-old nestling in 1970. A record of its molt was kept every year until 1980, except for 1971, when only a partial record was kept. The other owl (2A) was captured as a 4-month-old fledgling in 1976; its molt was subsequently recorded every year through 1980. During the molt, the plumage of both captive owls was examined every 7–10 days, and all molted feathers were collected and catalogued as they were shed.

RESULTS

Molt sequence during the first year of life.—When they hatched, owlets were sparsely covered by white natal down on most of the tracts that were occupied by contour feathers in adults. When owlets were 7–9 days old, their eyes opened, and, when they were about 10 days old, the juvenal plumage began to replace the natal down on the wings, back, and top of the head. Juvenal contour feathers were soft, fluffy, and pale brown with darker brown transverse barring (Fig. 1A). Natal down feathers were attached to the tips of many of the developing juvenal feathers. Replacement of the natal down by the juvenal contour feathers was essentially complete when owlets left the nest at 34–36 days of age (Fig. 1A).

The juvenal remiges became visible when nestlings were about 10 days old and reached full development at about 65 days. The rectrices became visible slightly later than the remiges and reached full development at about 75 days. When owlets left the nest, their remiges were about two-thirds developed and their rectrices were about one-fourth developed (Fig. 1A). As a result, owlets flew weakly for about 2 weeks after they left the nest and frequently resorted to climbing from one perch to another rather than flying.

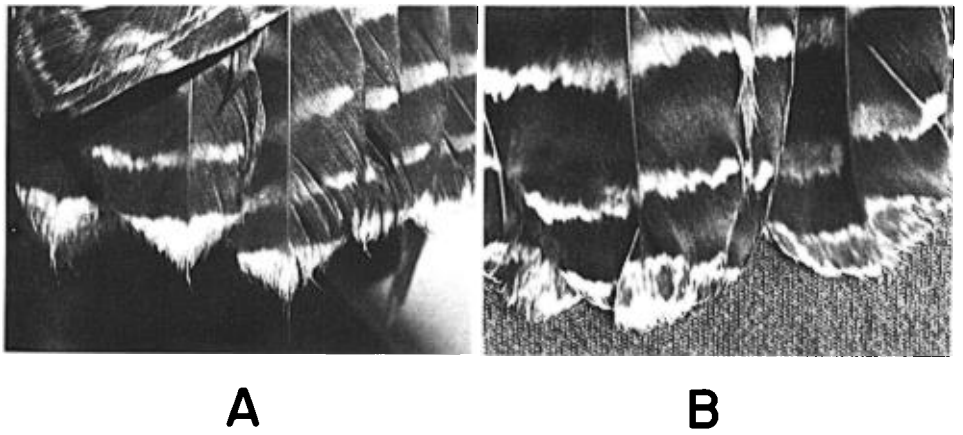

Fig. 2. Contrast between juvenal rectrices (A) and rectrices acquired in subsequent molts (B). Note white, slightly pointed tips of juvenal rectrices; rectrices acquired in subsequent prebasic molts had rounded tips that were not clear white.

Replacement of the juvenal contour feathers by the basic I plumage (prebasic molt) began at 47–56 days (between 1 June and 5 July) and was complete by late September or October. The only feathers not replaced during this molt were the juvenal remiges and rectrices and the greater primary coverts. The rate of molt was slow at first, reached a peak in July and August, then declined in September. With some minor differences, the prebasic molt followed the same pattern as described for young Screech Owls (*Otus asio*) by Kelso (1950). The molt began with the lesser, middle, and marginal wing coverts and progressed to the scapulars and greater wing coverts by the time owlets were 56 days old. At about the same time that the scapulars began to molt, feathers on the dorsal tract also began to molt. Between 57 and 67 days, molt of the wing coverts, back, and scapulars continued, and molt of the facial area and neck began. On the neck, the molt began near the posterior end of the interscapular tract and proceeded anteriorly. At 68–82 days, the scapulars and feathers on the back emerged rapidly, and the feathers on top of the head began to molt, beginning near the anterior end of the coronal tract and proceeding posteriorly and laterally. At 83–93 days, basic I feathers began to appear in two parallel rows down the sides of the breast, and the last greater wing coverts were molted. Between 94 and 120 days, the rows of feathers along the sides of the breast gradually merged to cover the entire ventral area, and the molt of the wings, back, and scapulars was completed (Fig. 1B). At 120 days, most feathers had been replaced on the neck and head except for a band of juvenal feathers across the back and sides of the head. By 135 to 155 days (10 September–15 October), the basic I plumage was complete (Fig. 1C).

Individuals in the basic I plumage were indistinguishable from adults, except that the tips of their rectrices were clear white and pointed. By comparison, rectrices acquired in subsequent molts had rounded tips that were white with brown blotches on the white background (Figs. 1C, 2). The white-tipped rectrices acquired in the first summer were not molted until owls were 26 months old and thus served as an age-specific marker for the first 2 yr of life (see below).

Molt sequence after the first year of life.—After their first year, both captive owls

TABLE 1. Order of primary molt in two captive Spotted Owls (1A and 2A).[a]

Year	1A	2A
1971	No data[b]	
1972	R 1,4,5,6,7,8,9,10	
	L 1,4,5,2,3,7,8,9,10	
1973	None molted	
1974	R 3,2,1,4,5,6,7,8,9,10	
	L 3,1,2,5,6,7,8,9,10	
1975	R 3	
	L 3,4	
1976	R 5,4,6,10	
	L 3,1,6,2,7,8,9	
1977	R 3,1,2,7,8,9	R 6,7,8,9,10
	L 3,1,6,2,7,8,9	L 6,9,10
1978[c]	R 2,4,5,6,10	R 1?,2,3,4,5
	L 2,4,5,10	L 1?,2,3,4,5,7,8
1979	R 4,7,8,9	R 1,6,7,8,9,10
	L 2,6,7,8,9	L 1,6,9,10
1980	R 2,3,1,5,6,10	R 4,5,2
	L 3,1,4,5,10	L 3,4,5,7,8

[a] Owl 1A was 1 yr old in 1971; 2A was 1 yr old in 1977.

[b] Owl 1A molted several primaries in 1971, but no record was kept of which ones they were. They were probably the ones not molted in 1972.

[c] A question mark after a primary number indicates that I was uncertain whether a primary was molted or not.

underwent an incomplete prebasic molt annually, beginning between 2 April and early June and ending in late September or October. The average duration of this molt (from first to last feathers shed) was 141 days (range = 112–184 days). During each prebasic molt, all of the body feathers were replaced in approximately the same order as in the first prebasic molt. Molt of the primaries, secondaries, and alulars occurred gradually and was incomplete; the typical pattern was the replacement of some of the feathers one year and the remaining feathers the next year (Table 1). This pattern was disrupted occasionally when one or more feathers were molted 2 yr in a row or were retained for 2 yr in a row. The pattern of molt of the remiges became increasingly complex as the owls grew older (Table 1).

The timing of the molt in wild and captive owls was similar. The earliest that I found molted feathers in Spotted Owl roost areas was 11 April. Adults trapped in mid-September frequently had some remiges and many feathers on the head and underwing areas in various stages of development, but by the end of October feather replacement was virtually complete.

Between 1976 and 1980, one of the captive owls (1A) laid infertile eggs each spring and incubated them for 30–60 days. In these years her molt did not begin until late May or June, nearly a month later than in years when she did not nest. Nesting females in the wild also appeared to molt few feathers until late May or June, when their young were 4–5 weeks old.

Regardless of which primaries were molted in a given year, primaries 4–10 virtually always molted in ascending order. The only instance in which this pattern was disrupted was when owl 1A molted primary 5 before primary 4 in one year (Table 1). Primaries 1–3 were molted in random order and were usually but not always molted before primaries 4–10 (Tables 1, 2). Corresponding primaries from opposite wings were molted in pairs 63% of the time; the remainder of the time they were molted in different years (Table 1). When corresponding primaries were molted in the same year, they were generally shed 0–10 days apart ($\bar{x}$ = 1.7 days). When adjacent primaries were molted in the same year, they were shed 8–55 days apart

TABLE 2. Dates when primaries were shed in both wild and captive Spotted Owls.[a]

Primary number	Range	Mode
1	21 April–7 August	May
2	13 May–17 September	May
3	13 May–15 July	May
4	4 May–17 June	June
5	24 April–23 June	June
6	17 May–16 August	June
7	3 July–27 August	July
8	21 July–5 September	August
9	18 August–14 September	August
10	14 July–7 September	September

[a] New primaries were fully developed 55–60 days after the old primaries were shed.

($\bar{x}$ = 17 days), leaving two or three feathers in different stages of regeneration at one time. The average rate of growth for regenerating primaries was 4.2 mm per day. Complete regeneration required 55–60 days.

I detected no consistent order in which the secondaries were molted in either wild or captive owls. The greatest number of secondaries molted by either of the captive owls in one year was 19 (range = 1–19). Corresponding secondaries in both wings were usually, but not always, molted in pairs.

All of the median, lesser, and marginal wing coverts were replaced each year between May and September, with the peak rate of molt occurring in July and August. The greater secondary coverts were molted between June and August; they were usually molted rapidly, leaving large gaps where two–nine adjacent coverts were shed during a few days. In both captive owls, the molt of these coverts was incomplete; it appeared that all were replaced at least once every 2 yr.

The upper greater primary coverts were molted gradually during the same period as the primaries. Usually, these coverts were molted along with their corresponding primaries, but primaries were occasionally molted without molt of their corresponding greater coverts, and vice versa. At least two prebasic molts were required to replace all of the greater primary coverts.

Molt of the greater coverts on the underside of the wing occurred between 28 June and 25 September, with the peak rate of molt in August. I did not determine if these coverts were molted completely each year.

Both captive owls molted their rectrices once every other year, beginning at age 26 months. All rectrices were molted one year; then none was molted the next year. This alternate-year molt pattern was adhered to strictly except for two consecutive years, when owl 1A molted no rectrices. In years when rectrix molt occurred, all 12 rectrices were shed rapidly during a period of 3–15 days ($\bar{x}$ = 9 days), leaving the birds without visible rectrices for about 10 days. This pattern was violated only once, when owl 2A molted all but one rectrix. The sequence in which rectrices fell out during these rapid tail molts followed no consistent pattern. The new rectrices developed relatively evenly, at an average rate of 3.7 mm per day, and were completely developed after approximately 55 days.

Thirty-three wild owls were seen in various stages of tail molt; three different patterns of replacement were noted: (1) a rapid and complete molt, as in the captive owls; (2) a disjunct, complete molt in which some rectrices fell out in May or early June and the rest fell out rapidly in late June or July, and (3) a partial molt. The

most common pattern apparently was a rapid and complete molt of the rectrices. I observed 17 adults (9 males, 7 females, and 1 sex unknown) that underwent such a molt, leaving them temporarily tailless. Eleven of the tailless individuals were seen between 15 and 31 July, indicating the peak period of rectrix molt. The latest bird to undergo a rapid tail molt was a male that had no visible rectrices on 24 August. The earliest was a male with all rectrices about two-thirds developed on 16 July (molt probably began about 14 June). The earliest date that molt of the rectrices began in the captive owls was 15 June, and the latest date was 11 August. The temporary absence of rectrices did not seem greatly to impair the flight of any of the owls observed.

Molt of the tail in two disjunct phases during a single season was apparently a common variation on the "simultaneous" molt pattern. Two adults were observed that lost one or two central rectrices in May or early June and then lost the rest very rapidly in late June or July.

Three radio-tagged females molted only part of their rectrices during the annual molt. One molted a single rectrix in early August, another molted 4 or 5 rectrices in August and early September, and another molted all but 2 of its rectrices during late July and August.

Like the captive owls, wild birds appeared to molt their rectrices only once every 2 yr. Many individuals were observed each summer that showed no sign of rectrix molt, and I concluded that these individuals were on an alternate-year molt cycle like the captive owls. I did not determine whether individuals undergoing a partial molt of the rectrices molted only those feathers that had not been replaced in the previous year (a pattern similar to the primary molt) or alternated between partial and complete molts in different years.

DISCUSSION

In young Spotted Owls, the plumage development from natal down to basic I followed a pattern similar to that reported for most other strigids (Sumner 1929, Bent 1938, Fleay 1942, Kelso 1950, Dement'ev et al. 1951, Collins 1961, Scherzinger 1980). The results of this study and studies by Weller (1965) and Piechocki (1974) demonstrated that at least some of the larger owls (*Bubo virginianus, Tyto alba, Strix occidentalis*) require 2 yr to replace all feathers. Statements to the contrary by Bent (1938), Dement'ev et al. (1951), and Oberholser (1974) were apparently based on surmise rather than data. Most smaller owls (e.g. *Strix aluco, Asio otus, Athene noctua, Micrathene whitneyi, Aegolius acadicus, Otus scops*), however, apparently do undergo a complete annual molt (Collins 1961; Ligon 1968; Piechocki 1968a, b, 1969). Apparently, the type of molt (complete or incomplete) is not predictable from phylogenic relationships. For instance, the Tawny Owl undergoes a complete annual molt (Piechocki 1968a), whereas the Spotted Owl molts on a 2-yr schedule.

To date, all studies of the molt in owls indicate a complete annual molt of the body feathers. Apparently, a complete molt of the body feathers is required to insure maximum insulative efficiency during the fall and winter. Because the remiges and rectrices play only a minor role in thermoregulation, it is probably not critical that they be molted every year, at least from a thermoregulatory standpoint. The incomplete molt of the remiges and rectrices has probably evolved because it reduced the energy expenditure associated with the molt. Why an incomplete molt occurs only in larger owls, however, is unknown.

The tail molt in owls has received considerable attention since Mayr and Mayr (1954) presented evidence that small owls usually molted the tail feathers simultaneously, whereas large owls molted the rectrices gradually or irregularly (Verheyen 1956; Collins 1961; Courser 1972; Piechocki 1968a, b, 1974). Mayr and Mayr (1954) were incorrect, however, in their belief that molt of the rectrices was gradual in *Strix*. In addition to the Spotted Owl, it is now known that rapid molt of the rectrices occurs in the Tawny Owl (Piechocki 1968a) and at least occasionally in the Barred Owl (*Strix varia*) (David L. Evans pers. comm., Mark R. Fuller pers. comm.).

Based on my experience with Spotted Owls and a review of the literature, I believe that the word "simultaneous" should be used sparingly with respect to the tail molt in owls, because it appears that the molt is rarely simultaneous; rather, the feathers are shed *rapidly* during a period of several days or weeks. Regardless of whether the feathers are shed in 1 day or over a 2-week period, the effect is the same—the owl is left without a functional tail for some time. The advantages of this type of molt in owls are unknown. Mayr and Mayr (1954: 178) suggested that complete taillessness during a short period might be "biologically less advantageous" than a gradual molt but did not suggest what the advantages might be.

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ERRATA

Through an editorial oversight, two corrections in the galleys of the paper "Effects of abundant species on the ability of observers to make accurate counts of birds," by J. Michael Scott and Fred L. Ramsey (1981, Auk 98: 610–613), were not incorporated into the final published version. Please make the following corrections:

1. Page 610, paragraph 3, line 7: the scientific name for the Akiapolaau should read *Hemignathus wilsoni,* not *Hemignathus obscurus.*

2. Page 610, paragraph 5: the second sentence should read ". . . the radius as specialist exceeded that as generalist for Apapane (4 out of 5 cases) and Hawaiian Thrush (4 out of 5 cases).", not "In 6 of 8 cases and 5 of 8 cases the radius as specialist exceeded that of generalist for Apapane and Hawaiian Thrush, respectively."