The Auk 121(1):35–45, 2004

POLYMORPHIC FLIGHT-FEATHER MOLT SEQUENCE IN TUFTED PUFFINS (*FRATERCULA CIRRHATA*): A RARE PHENOMENON IN BIRDS

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Abstract.—Previous reports have stated that Tufted Puffins (*Fratercula cirrhata*) lose all of their flight feathers simultaneously (or nearly so) during flight-feather molt and replace them in no apparent order. In contrast, we found that captive second-year (SY) Tufted Puffins (1) typically require 15 and 10 days to lose their primaries and secondaries, respectively, during their first flight-feather molt, and an average of 21 days to lose all of their remiges; and (2) replace their primaries in either of two discrete sequences. In 9 of 13 birds, primary molt began at the innermost primary, P1, and progressed distally to the outermost functional primary, P10. However, in the remaining four birds, primary molt began in the middle of the primaries (P5–P7) and progressed both distally to P10 and proximally toward P1. Before the proximal wave reached P1, a second wave of molt was initiated at P1 and progressed distally, typically replacing P2 and P3 before reaching the proximal wave. Such polymorphism in flight-feather molt sequence is rare in birds, having been reported previously only in a few passerine species. Secondary molt began about 13 days after onset of primary molt and finished at about the same time as primary molt, resulting in a total duration of flight-feather molt of ~54 days and a flightless period of ~40 days. *Received 6 December 2001, accepted 7 September 2003.*

Resumen.—Se ha establecido mediante reportes previos que las aves de la especie *Fratercula cirrhata* pierden todas sus plumas de vuelo simultáneamente (o casi) durante la muda de las plumas de vuelo, y que las reemplazan sin un orden aparente. En contraste, nosotros encontramos que individuos cautivos en su segundo año (1) requieren típicamente 15 y 10 días para perder sus plumas primarias y secundarias, respectivamente, durante su primera muda de las plumas del vuelo, y un promedio de 21 días para perder todas sus remeras; y (2) reemplazan sus primarias en cualquiera de dos secuencias discretas. En nueve de 13 aves, la muda de las primarias comenzó en la primaria más interna, P1, y progresó de modo distal hacia la primaria funcional más externa, P10. Sin embargo, en las cuatro aves restantes la muda comenzó en las primarias de la mitad (P5–P7) y progresó de modo distal hacia P10 y proximal hacia P1. Antes de que la onda proximal llegara a P1, una segunda onda de muda se inició en P1 y progresó de modo distal, reemplazando típicamente a P2 y P3 antes de alcanzar la onda proximal. Este polimorfismo en la secuencia de muda de las plumas del vuelo es raro en las aves, y ha sido reportado previamente sólo para unas pocas especies de paserinos. La muda de las secundarias comenzó aproximadamente 13 días después del comienzo de la muda de las primarias y terminó casi al mismo tiempo que la muda de las primarias, resultando en una duración total de la muda de las plumas del vuelo de ~54 días y en un período de incapacidad de vuelo de ~40 días.

Molt, especially of flight feathers, is an energetically expensive and time-consuming activity in the annual cycle of birds (Walsberg 1983, Murphy and King 1991, Murphy 1996, Klasing 1998). In addition, during flight-feather molt, the ability to fly is diminished by increased wing loading and by gaps in the wing where flight feathers are missing or regrowing, thereby increasing flight costs and vulnerability to predators. As a result, various aspects of the molting process are subject to strong natural selection. The tremendous diversity observed in (1) the site(s) at which flight-feather molt is initiated and (2) the sequence in which flight feathers are replaced in various species (Dwight 1900, 1925; Stresemann and Stresemann 1966;

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Ginn and Melville 1983; Baker 1993; Jenni and Winkler 1994; Pyle 1997a; Rohwer 1999) probably reflects both strong selection pressure and differences in species' life histories.

For example, most species of diving birds (e.g. loons [Gaviidae], most grebes [Podicipedidae], diving petrels [Pelecanoididae], darters and anhingas [Anhingidae], most waterfowl [Anseriformes], and medium-size to large alcids [Alcidae]) molt during the nonbreeding season while living on the ocean or other bodies of water. The literature regarding molt in those groups generally states that they lose all their remiges simultaneously or nearly so, implying that regrowth of remiges is also synchronous—that is, they are not replaced in any apparent order (Palmer 1962, 1972, 1976a, b, 1988a, b, 1988; Stresemann and Stresemann 1966; Cramp 1977, 1980, 1983, 1985, 1988, 1992, 1993, 1994a, b; Marchant and Higgins 1990a, b, 1993; Wells 1999). In contrast, Thompson et al. (1998) recently found that Common Murres (*Uria aalge*) lose and replace their primaries rapidly but not simultaneously, and do both in a consistent, orderly fashion. Especially interesting is the unusual sequence of loss and replacement: primary molt begins at a single node in the middle of the primaries and proceeds in two concurrent waves, one proximally to P1 and the other distally to P10. However, it is not known whether the sequence of flight-feather molt observed in Common Murres occurs in any other alcids or in other diving birds.

The purpose of our study was to investigate the sequence of flight-feather molt in another large alcid, the Tufted Puffin (*Fratercula cirrhata*). Compared to Common Murres, which weigh ~1 kg (Ainley et al. 2002) and are remarkably monomorphic in body size and mass, Tufted Puffins are slightly lighter (750–800 g) and more sexually dimorphic (Shiomi and Ogi 1991), with males averaging 4–7% larger than females (Piatt and Kitaysky 2002a). Tufted Puffins breed only in the eastern and western North Pacific from California, Oregon, Washington, British Columbia, the Gulf of Alaska, and the Bering and Chukchi Seas, westward across the Aleutian Islands to the Sea of Okhotsk, the Kuril Islands, and Japan. Given their relatively extensive breeding distribution, a great deal is known about most aspects of Tufted Puffin ecology. However, among alcids, including other puffin species, Tufted Puffins are the most pelagic; as a result, remarkably little is known about aspects of their life history during the nonbreeding season, including their molts (Piatt and Kitaysky 2002a). Therefore, our specific goals here are twofold: (1) to provide a detailed description of seasonal timing, rate, and sequence of flight-feather molt in Tufted Puffins; and (2) to briefly discuss the potential functional significance, if any, of the observed sequence and rate of molt.

Materials and Methods

Collection and husbandry of Tufted Puffin eggs and chicks.—Partially incubated eggs of free-living Tufted Puffins were collected from a colony of seabirds in Lower Cook Inlet, Alaska, and transported to the University of Washington facilities. Eggs were incubated using Lyon incubators at 37.1°C and 56% relative humidity until hatching. Chicks were raised in individual nests at 28°C and 80% relative humidity to seven days, then at 20°C and 70% relative humidity until fledging, and at outdoor ambient temperature and humidity at the University of Washington thereafter. Chicks were fed capelin (*Mallotus vilosus*) with an excess of multimineral and vitamin supplement (one tablet per day of USP-quality Kirkland Signature, Kirkland, Washington) in their food. After the study ended, the nine-month-old birds were transferred to the Lincoln Park Zoo (Chicago) and Bronx Zoo (New York) for captive breeding programs and permanent exhibition.

Measuring length of growing flight feathers.—Rectrices and remiges on both wings of each bird were examined on 12 occasions in spring 2000 (6, 10, 14, 16, 21, 24, 28, and 31 March, and 4, 12, 16, and 25 April). Each flight feather was examined to determine whether it was old (juvenal), growing, or new and full grown. The length of each growing remex was measured by inserting a ruler between and parallel to the remex being measured and the next more distal remex, and gently pushing the end of the ruler up to the point where the base of the remex being measured emerged from the feather follicle. Then, by laying the remex along the length of the ruler, its length was measured to the nearest millimeter. The mean difference in length between adjacent growing primaries varied among pairs of primaries from a minimum of 2.6 ± 0.2 mm between P2 and P3 to a maximum of 7.1 ± 0.4 mm between P8 and P9 (Fig. 1). On both the right and left wings of each bird, the longest growing primary was assigned a rank of 1, the next longest was assigned a rank of 2, and so on. Within each wing of each bird, the order in which growing primaries were ranked never changed.

Calculating primary and secondary molt scores.—Primaries and secondaries are numbered from the innermost (P1) to outermost (P10, not including vestigial

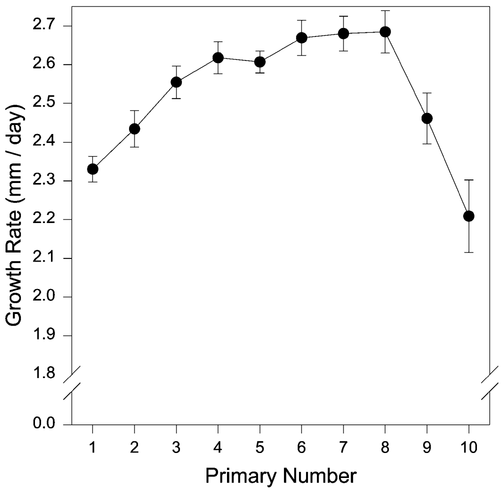

FIG. 1. Growth rate (mean ± SE) of primaries 1–10 of 13 captive Tufted Puffins during their first flight-feather molt.

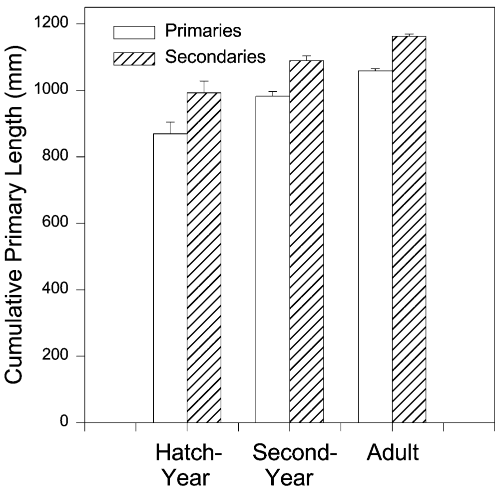

FIG. 2. Cumulative length of all primaries and secondaries in hatch-year, second-year and adult Tufted Puffins (sexes combined).

P11), and outermost (S1) to innermost (usually S18), respectively. Rectrices are numbered from the central pair (R1) to the outermost pair (R7). To calculate the flight-feather molt score of a molting bird, it is necessary to accurately estimate how long each flight feather will be when it is fully grown. In most species of birds, the mean length of adult (definitive *sensu* Humphrey and Parkes 1959) flight feathers is greater than that of previous generations of flight feathers (Pyle et al. 1997). Therefore, using extended-wing specimens in the Burke Museum at the University of Washington of nonmolting hatch-year (HY), SY, and older male (n = 2, 3, and 21, respectively) and female (n = 3, 4, and 14, respectively) Tufted Puffins (i.e. that had replaced their juvenal primaries), I measured the length of each of the 10 functional primaries and 18 secondaries (C. W. Thompson unpubl. data) with a ruler to the nearest 0.5 mm from the point of insertion in the skin to the terminal end of each feather. For each bird, lengths of primaries and secondaries were summed to give cumulative lengths of all primaries and secondaries, respectively. Two-way repeated-measures ANCOVAs using age and sex as factors and primary and secondary number as covariates indicated that absolute (but not relative) primary and secondary lengths (i.e. total wing size) differ significantly among age classes but not between sexes (age: $F \geq 28.97$, df = 2 and 41, $P < 0.001$; sex: $F \leq 1.23$, df = 1 and 41, $P \geq 0.27$). Subsequent Fisher's least significant difference *post-hoc* tests revealed that primary and secondary lengths are greater in adults than in SY birds ($P < 0.001$) which, in turn, are longer than those of HY birds ($P < 0.017$). As a result, two-way ANOVAs using age and sex as factors also indicated that cumulative lengths of primaries and secondaries did not differ between sexes ($F \leq 0.369$, df = 1 and 41, $P \geq 0.547$), but did differ among age classes (Fig. 2; $F \geq 30.53$, df = 2 and 41, $P < 0.001$). For molting birds, all growing remiges were measured in the same fashion. Old feathers received a score of 0; empty follicles were assigned a value of 0.1 mm to indicate that the old feather was lost. As above, all values were summed to give a cumulative measure of flight-feather growth. Primary-molt score for each molting bird was calculated as a percentage of total regrowth: (cumulative primary growth of molting bird / mean total primary length of nonmolting SY bird) × 100; the minimum molt score being 0.01, and the maximum being 99.99. Secondary-molt score was calculated in analogous fashion. Rectrix molt was noted, and the length of the longest growing rectrix, if any, was measured, but molt score was not calculated for the rectrices.

Determination of flight-feather molt sequence.—During molt, old flight feathers are actively pushed out by new feathers that replace them (Watson 1963a, b; Wolf 1967). Thus, the sequence in which flight feathers are lost reflects the sequence in which they are replaced and vice versa (e.g. follicles from which the first primary and secondary appear on each wing are the follicles at which primary and secondary molt are initiated, respectively). Within individual birds, including Tufted Puffins (Fig. 1), growing remiges increase in length during molt at a relatively uniform rate. However, in most birds, including Tufted Puffins, remiges that are longer when fully grown often grow at a slightly greater rate than remiges that are shorter when fully grown (Underhill and Zucchini 1988; Fig. 1). In addition, the growth rate of each feather decreases as it approaches its fully grown length. However, those sources of variation are minor relative to the mean absolute growth rate of remiges. Therefore, absolute differences in length between adjacent growing primaries (discussed above) remain quite constant until feathers are at least 80% fully grown. As a result, absolute remex length in Tufted Puffins is a reliable index of remex age, at least until feathers approach their fully grown length. Thus, within each set of flight feathers (primaries and secondaries), in the early stages of feather regrowth before any remiges are nearly full-grown, the first primary or secondary in the molt sequence can be operationally identified as the longest growing feather (rank = 1); the second feather in the molt sequence is the next-longest growing feather (rank = 2), and so on. As a result, primary and secondary molt sequence is indicated both by the sequence in which these feathers are lost, and by the sequence in which they are regrown.

Estimating rate of loss of primaries and secondaries.—Because birds were examined only once every two to nine days (see below), a bird may have lost its first primary one to eight days before the loss was noted. On each occasion when the loss of one or more primaries was first observed, if no new growing primaries were visible, then that date was accepted as the beginning of primary molt. However, if one or more new growing primaries were visible, the longest one was measured. The next time the bird was examined, that feather was measured again and its growth rate was calculated as the difference in the length of the primary between the two dates, divided by the number of days between dates. Using this growth rate, the number of days required for the longest new primary to reach its length on the first date it was observed and measured was calculated, and the initial date on which new primary growth most likely first appeared was estimated by counting back that many days. An analogous process was used to estimate the date on which the last primary was lost, and for tracking the loss of secondaries as well. The time necessary for loss of all primaries and secondaries was estimated for all but one bird that had not lost all of its remiges before the end of the study.

Statistics and estimating flight-feather molt duration.—Statistics were conducted using SYSTAT 10 (SPSS, Chicago, Illinois). Values are presented as mean ± SE. Methods used to score primary and secondary molt (described above) yield molt scores that increase linearly over time and, therefore, are ideal for accurately estimating duration of flight-feather molt using linear regression. Because primary and secondary molt were scored repeatedly (6.6 ± 0.6, $n = 12$, and 5.1 ± 0.8, $n = 10$, respectively) on individual birds, date of onset and duration of primary and secondary molt were estimated by regressing molt score on date for each of those birds. The R^2 values of regressions of primary and secondary molt scores on date were 0.965 ± 0.006 and 0.966 ± 0.008, respectively, reflecting the linear nature of remigial growth and the accuracy of our molt scoring methodology for quantifying flight-feather molt. A two-sample t-test with pooled variances was used to test for difference in rate of loss of primaries in birds that initiated primary molt at one versus two nodes. A paired t-test was used to test for a difference in rate of loss of primaries versus secondaries within individual birds during flight-feather molt. Timing of onset of secondary molt in relation to primary molt was determined for each of 10 individual birds for which we had measures of primary and secondary molt from a minimum of three different days by regressing their secondary molt scores on their primary molt scores. Results were considered statistically significant when $P < 0.05$.

RESULTS

Primary molt sequence.—Tufted Puffins replaced their juvenal primaries in either of two basic sequences. The most common sequence was for primary molt to begin at P1 and proceed distally in sequence to P10. That pattern was exhibited by 9 (6 males, 3 females) of the 13 birds; one of those birds had lost P1–P5 and had begun growing P1 on the left side but was not followed further because the study ended. The alternative sequence exhibited by four birds (one male, three females) was for primary molt to begin in the middle of the primaries and proceed in two concurrent waves—one proximally toward P1, the other distally to P10. Between 0 and 9 days after primary molt began in the middle of the primaries, primary molt was initiated at a second node, P1, and progressed distally toward the wave that was advancing proximally from the middle of the primaries. The central node was located on the two wings at P5 and P6 in one bird, P6 on another bird, and P6 and P7 on a third bird. The fourth bird was especially unusual in that it replaced primaries in the more typical sequence from P1 through P10 on its right wing, but by the alternate sequence on its left wing, its central node being at P5 on that wing.

Secondary molt sequence.—Secondary molt began, on average, 13.2 ± 0.9 days after onset of primary molt when primary molt was 23.4 ± 2.5% completed, but 4.2 ± 1.5 days before the last primary was lost. The order in which secondaries were lost and replaced was less clear than the primary molt sequence. In all 12 birds that exhibited secondary molt before the end of the study, the first secondary to be lost and show visible regrowth was the outermost secondary, S1; secondary molt proceeded proximally from this point. The order in which other secondaries were lost and regrown was highly variable within and among birds. In general, birds tended to lose their innermost secondaries next, from a molt center located between S14 and S18, molt proceeding both distally and proximally (unless the node was located at the innermost secondary, S18). There also appeared to be a third node at S5, but the highly variable lengths of the growing secondaries made it difficult to discern such patterns with certainty.

Rectrix molt.—Rectrix molt began when primary molt was 55–85% complete, and when the longest primaries were about 65–80 mm in length; it was completed shortly before or at the same time as remigial molt.

Rate of loss of primaries and secondaries.—All juvenal primaries were lost in about two weeks (15.3 ± 1.7 days). However, birds that initiated primary molt at two nodes rather than a single node (discussed below) lost all of their primaries in fewer days, on average—in 12.0 ± 3.5 days versus 16.9 ± 1.7 days, respectively, although that difference was not statistically significant ($t = 1.4$, df = 10, $P = 0.18$). Birds lost all of their juvenal secondaries more rapidly than their primaries ($t = 2.46$, df = 11, $P = 0.032$), taking only 10.3 ± 0.8 days. Before the last juvenal primary was lost, on each wing (1) an average of 5.6 ± 0.7 new primaries exhibited visible growth, the longest of those averaging 25.0 ± 3.8 mm in length; (2) a minimum of 2.2 ± 1.2 (range = 0–13) secondaries were shed; and (3) a minimum of 1.0 ± 0.6 new secondaries exhibited visible growth, the longest of those averaging 2.2 ± 1.3 mm in length. By the time regrowth of the first new secondary (S1) became visible, the longest primary averaged 29.4 ± 3.1 mm. In addition, because secondaries were lost more rapidly than primaries, regrowth of secondaries was more synchronous. As a result, before the last juvenal secondary was lost, an average of only 3.5 ± 1.5 new secondaries exhibited visible growth, the longest of those averaging 11.3 ± 2.0 mm in length. In addition, because secondary molt began 4 days, on average, before the last primary was dropped, total duration of time between loss of the first primary and loss of the last secondary was 20.8 ± 1.7 days, on average.

Seasonal timing and duration of molt.—Birds hatched on 27 July (±2.4 days) and began primary and secondary molt the following spring at 235 (±4.2) and 248 (±3.8) days of age, respectively, corresponding to 21 March (±4.0 days, range = 22 February to 25 April) and 3 April (±3.9 days, range = 9 March to 19 April). Primary and secondary molt were completed 53 (±2.8, range = 42–60) and 38 (± 1.9, range = 32–50) days later on 13 May (± 5.3 days, range = 23 April–26 June) and 7 May (± 3.9, range = 23 April–26 June), respectively. Because secondary molt finished at the same time, on average, as primary molt within individual birds, the total duration of primary and secondary molt was 53.6 ± 3.1 days—that is, it was essentially identical to the duration of primary molt alone.

Discussion

Potential effects of captivity on molt.—Various factors—such as food abundance and quality, temperature, photoperiod, and presence or absence of stressors—can clearly influence the seasonal timing, rate, and extent of molt, and even the color of plumage grown during molt (Thompson 1999). Effects of captivity may influence the frequency of molt. For example, Swennen (1977) found that some captive Atlantic Puffins (*F. arctica*) replaced their flight feathers twice in their second and third calendar years of life, but only once each year thereafter, whereas other individuals replaced their flight-feathers only once in their second calendar year of life and thereafter. Whether that variability also occurs in nature or was the result of captivity is unknown. Likewise, the results reported here may or may not reflect the rate and timing of the first flight-feather molt in Tufted Puffins in nature.

However, there is no evidence that captivity influences molt sequence, nor can we imagine a physiological mechanism whereby maintenance of birds under captive conditions that are reasonably similar to conditions in nature could potentially do so.

Primary molt sequence.—Polymorphism in the sequence of primary molt is rare in birds, having been documented, to our knowledge, only in five species of passerines: Eurasian Jay (*Garrulus glandarius*; Bährmann 1971), Rook (*Corvus frugilegus*; Dorka [1971] *in* Jenni and Winkler 1994), Brown Shrike (*Lanius cristatus*; Stresemann and Stresemann 1971), Savi's Warbler (*Locustella luscinioides*; Steiner 1970, Mead and Watmough 1976, Thomas 1977, Müller 1981, Bensch et al. 1991), and Richard's Pipit (*Anthus richardi*; Stresemann and Stresemann 1968). We found that Tufted Puffins also exhibit a polymorphism in primary molt sequence; captive SY males and females from a single population exhibit two discrete primary molt sequences during their first flight-feather molt. In the more common sequence, primary molt begins at P1 and proceeds distally to P10. That is by far the most common primary molt sequence in both passerine and nonpasserine birds (Dwight 1900, 1925; Stresemann and Stresemann 1966; Palmer 1962, 1972, 1976a, b, 1988a, b; Cramp 1977, 1980, 1983, 1985, 1988, 1992, 1993, 1994a, b; Marchant and Higgins 1990a, b, 1993; Jenni and Winkler 1994; Higgins and Davies 1996; Pyle 1997a; Higgins 1999; Higgins et al. 2001), including most seabirds (Palmer 1962; Ashmole 1971; Warham 1990, 1996; Johnsgard 1993; Gaston and Jones 1998; Tickell 2000). The other primary molt sequence exhibited by Tufted Puffins begins in the middle of the primaries (P5, P6, or P7) and proceeds in two concurrent waves, one proximally toward P1 and the other distally to P10; at the same time, or up to nine days after primary molt is initiated in the middle of the primaries, primary molt is initiated at another node, P1, and proceeds distally, where it meets the wave proceeding proximally from the middle of the primaries at a point between the two nodes.

Among alcids, initiation of primary molt in the middle of the primaries followed by replacement of primaries in two concurrent waves, one proceeding distally and the other proximally, has been documented only in Common Murres (Thompson et al. 1998), but published data suggest that the pattern also occurs in Kittlitz's Murrelet (*Brachyrampus brevirostris*; see table 1 in Sealy 1977), contrary to Sealy's (1975, 1977) statements that their remigial molt is "simultaneous," and in Black Guillemots (*Cepphus grylle*; Braune 1987); and that it occurred in Great Auks (*Pinguinus impennis*; Salomonsen 1945, Storer 1960, Stresemann and Stresemann 1966) as well. Among other avian taxa, that molt pattern (known as "Hampe's rule" after H. Hampe; Stresemann and Stresemann 1966) occurs in all parrots (Psittaciformes; Rowley 1988, Forshaw and Cooper 1989), all falcons (Falconidae; Donner 1907; Dement'ev 1940, 1960; Piechocki 1956, 1963; Sutter 1956; Stresemann 1958; Mebs 1960; Stresemann and Stresemann 1960, 1966; Willoughby 1966; Glutz von Blotzheim and Bauer 1982; Ginn and Melville 1983; Cramp 1985; Palmer 1988a, b; Johnsgard 1990; Baker 1993; Marchant and Higgins 1993), barn owls and their allies (Tytonidae; Piechocki 1974; Schönfeld and Piechocki 1974; Ginn and Melville 1983; Lenton 1984; Cramp 1985; Taylor 1994; Pyle 1997a, b; Higgins 1999; Wells 1999), one species of kingfisher (Pied Kingfisher, *Ceryle rudis*; Douthwaite 1971, Sugg 1974; *contra* Stresemann and Stresemann 1961), and some individuals in the five passerine species mentioned above. The same molt sequence has been described for some hummingbirds (Wagner 1955) as well, though subsequent work on many of the species that Wagner (1955) studied suggest that his conclusions were incorrect, perhaps because of methodological errors (Russell et al. 1994; Scott 1994; Pyle 1995, 1997a; Stiles 1995; Pyle et al. 1997).

However, none of the above-mentioned species also initiate molt at P1, as Tufted Puffins do. The only species documented to exhibit that pattern of primary molt are the Belted Kingfisher (*Ceryle alcyon*), a member of the same subfamily, Cerylinae, to which the Pied Kingfisher belongs (Stresemann and Stresemann 1961, 1966; Cramp 1985; Hamas 1994; Pyle 1995), and some large typical owls (Strigidae, e.g. Eagle Owls [*Bubo bubo*], Brown Fish Owls [*Ketupa zeylonensis*], and Snowy Owls [*Bubo scandiaca*]; Ginn and Glue 1974; Cramp 1985; Pyle 1997a, b; Higgins 1999; Wells 1999).

Secondary molt sequence.—Secondary molt began at the outermost secondary, S1, and proceeded proximally and much more rapidly than primary molt. Shortly after molt began at S1, molt appeared to be initiated between S14 and the innermost secondary, S18, and probably progressed distally and proximally (unless initiated at S18). Some birds appeared to have a third node around S5. That is somewhat expected because alcids are diastataxic—that is, through evolution they have lost S5 so that their current S5 is actually homologous with S6 in eutaxic birds (Bostwick and Brady 2002). Most, but not all, diastataxic taxa have a secondary molt node at S5, for example, many procellariiform seabirds (Warham 1990, 1996; Thompson et al. 2000), cormorants (C. W. Thompson unpubl. data), some owls (e.g. *Strix*, *Asio*; Cramp 1985, Pyle 1997b, Higgins 1999), some hawks (Miller 1941, Cramp 1980, Marchant and Higgins 1993), some large terns (C. W. Thompson unpubl.

data), some kingfishers, and some hummingbirds (Stresemann and Stresemann 1966).

Rate of loss of primaries and secondaries.—Few comments exist in the literature regarding the rate or sequence of flight-feather molt in Tufted Puffins or other puffin species. Hamilton (1958) stated that remigial molt in Tufted Puffins involves a "complete and simultaneous shedding of the primaries." Similarly, loss of remiges in Atlantic Puffins has been described as occurring "almost simultaneously" (Lockley 1953), "more or less synchronously" (Harris 1984), and "simultaneously" (Bureau [1879] *in* Stejneger 1885, Cramp 1985, Lowther et al. 2002). However, we found that it takes three weeks on average for the birds to lose all of their remiges, that primary molt is nearly one-quarter completed before secondary molt begins, and that at least half of the birds show visible growth of new secondaries before the last old primary is shed. Atlantic Puffins molt similarly in that they do not lose their secondaries until "the primaries have just broken through their sheath," and secondaries do not emerge from the follicles until primaries are 20–30 mm in length (Harris and Yule 1977). However, in contrast to Tufted Puffins—which often shed many secondaries before dropping their last primary—Atlantic Puffins, like Common Murres (Thompson et al. 1998), do not lose any secondaries until after all of their primaries have dropped (Gerbe 1875, Stresemann and Stresemann 1966, Harris and Yule 1977). No description of flight-feather molt sequence or rate exists for Horned Puffins (*F. corniculata*; Bent 1919, Dement'ev and Gladkov 1951, Flint and Golovkin 1990, Piatt and Kitaysky 2002b).

Seasonal timing and duration of molt.—All birds began their first flight-feather molt between late February and late April of their second calendar year and completed it 6–8 weeks later, between late April and late June. Birkhead and Taylor (1977) estimated that Common Murres, and presumably other large alcids, do not regain aerial flight ability until flight-feather molt is about 70–80% fully grown. That implies a flightless period for Tufted Puffins of ~40 (range 32–45) days.

Data regarding seasonal timing of flight-feather molt in Tufted Puffins and other puffin species, especially of subadult age classes, is both scant and confusing (e.g. Witherby et al. 1941, Salomonsen 1944, Lockley 1953, Harris and Yule 1977, Swennen 1977, Harris 1984, Cramp 1985, Lowther et al. 2002, Piatt and Kitaysky 2002b). Regarding Tufted Puffins, Bent (1919) stated that flight-feather molt occurs in SY birds in August and September, but presented no data to support his claim. In contrast, both Kuroda (1955) and Stresemann and Stresemann (1966) state that SY birds molt in June and provide specimen data to document their assertions. That suggests that our captive SY birds molted their juvenal flight feathers on a schedule similar to that of Tufted Puffins in the wild.

Very little is known about molt in seabirds that molt at sea during the nonbreeding season. The only practical way to study molt in detail in those species in the wild is to (1) actively collect them at sea for such studies, as noted by Harris and Yule (1977), which we do not generally advocate; or (2) use specimens that were collected for other studies or killed incidentally—for example, in oil spills or fisheries operations (gill nets, drift nets, long lines, etc.; Thompson et al. 1998)—or found beach-cast, having died from various causes (Thompson et al. 2000). There are substantial political, legal, logistical, and financial difficulties in undertaking any such studies. However, as demonstrated here, many questions regarding molt in seabirds can be inexpensively, efficiently, and accurately studied on captive birds. Therefore, we encourage others to study molt in alcids and other seabirds by collaborating with zoos, aquaria, and others around the world that house such species (Gunther 1994).

ACKNOWLEDGMENTS

This article is dedicated to the life and memory of C.W.T.'s brother-in-law, Rory Simm, who loved birds, shared his birding experiences and interests with C.W.T., and facilitated many memorable birding trips by C.W.T. in his Irish homeland. We thank Z. Kitaiskaia for raising the Tufted Puffins; L. Erckmann and L. Wright for help with husbandry; J. Wingfield and J. Piatt for logistic support; M. Leu for translating German references for us; and M. Benowitz-Fredericks, V. Friesen, D. Nettleship, K. Smith, and three anonymous reviewers for providing helpful comments on earlier drafts of the manuscript. Financial support for this study was provided by the Exxon Valdez Oil Spill Trustee Council (Restoration project #99479 to A.S.K.). Work with birds in captivity was accomplished according to the guidelines of the Laboratory Animal Care and Use Protocol of the

University of Washington, and under federal and state collection permits.

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Associate Editor: D. N. Nettleship