

## AN UNUSUAL SEQUENCE OF FLIGHT-FEATHER MOLT IN COMMON MURRES AND ITS EVOLUTIONARY IMPLICATIONS

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**ABSTRACT.**—Common Murres (*Uria aalge*) exhibit an unusual molt sequence. Primary molt begins at a focus between P4 and P7 and progresses in two rapid concurrent waves, proximally to P1, and distally to P10. The only other birds known to have a similar molt sequence are caracaras and falcons (Falconidae), parrots (Psittaciformes), and Pied Kingfishers (*Ceryle rudis*). Great Auks (*Pinguinus impennis*) also appear to have followed the same primary-molt sequence. Phylogenies for the Alcidae indicate that Great Auks, Common Murres, Thick-billed Murres (*Uria lomvia*), Razorbills (*Alca torda*), and Dovekies (*Alle alle*) share a common ancestor and are more closely related to one another than to other alcids. This suggests that the unusual sequence of primary molt in Common Murres is a shared-derived character that occurs in the other four species in their clade but has been overlooked. Adult male Common Murres have significantly shorter secondaries and longer primaries, on average, than do adult females, resulting in a slightly higher aspect ratio in males. Secondary molt begins when primary molt is more than one-third completed. Secondaries are replaced rapidly but sequentially (not synchronously or simultaneously); molt appears to proceed from two foci, proximally from S1 to S4, and both proximally and distally from S8, but more data are needed to clarify this point. Rectrix molt begins when primary molt is two-thirds completed. Rectrix loss and replacement occur rapidly, possibly synchronously, and in no apparent order. Adults molt about two weeks later than nonbreeding subadults. We found no differences in the timing of molt between the sexes in adults or subadults. Duration of flight-feather molt can vary from less than 25 days to more than 80 days, possibly reflecting interyear variation in prey abundance. Received 12 February 1997, accepted 9 December 1997.

RELATIVE TO MOST OTHER TOPICS in ornithology, virtually all aspects of the molting process are poorly documented and understood (Pyle et al. 1987, Jenni and Winkler 1994). This is especially true in seabirds because most species, including all species that become flightless during molt, undergo molt at sea during the nonbreeding season (Palmer 1962, Glutz von Blotzheim and Bauer 1982, Cramp 1977, 1983, Warham 1996). Among alcids, molt has been better studied in Common Murres (*Uria aalge*) than in many other species (Verwey 1922, 1924, Salomonsen 1944, Stresemann and Stresemann 1966, Birkhead and Taylor 1977), but many aspects of their molt remain poorly known (contra Harris and Wanless 1990).

As an extension of studies on seabird entanglement in gill nets in Puget Sound (Thompson et al. 1998), we studied molt in Common

Murres. The phenology of breeding in Common Murres differs by two months or more among geographic areas. Thus, flight-feather molt scores in postbreeding adults might be useful for identifying breeding location (e.g. Oregon vs. Washington); this is important for determining the demographic effect of mortality caused by gill nets or other anthropogenic activities on different breeding populations of Common Murres.

### MATERIALS AND METHODS

In 1993, commercial gill net fisheries occurred for summer sockeye salmon (*Onchorhynchus nerka*) in northern Puget Sound and for fall chum salmon (*O. keta*) in Hood Canal and central Puget Sound, Washington (Pierce et al. 1994). To evaluate various modified gill net designs, test fisheries were done in 1993 by Washington Sea Grant, and in 1993 and 1996 by Washington Sea Grant and Washington Department of Fish and Wildlife. Entangled seabirds were collected: (1) from commercial fisheries in 1993 from 1

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August to 5 September and 5 October to 23 November; and (2) from test fisheries in 1993 from 6 July to 1 August, and 2 September to 5 October (Boessow 1996), and in 1996 from 28 July to 29 August (Melvin et al. 1997).

Data collected included bill length, body mass, plumage coloration, status of flight-feather molt, size and physical description of bursa of Fabricius, gonad size, and presence or absence of an incubation patch; in females, the largest follicle in the ovary was measured, and oviduct condition was noted. Bursa condition was categorized into one of three categories: (1) large and fleshy; (2) thin-walled; or (3) membranous, or no bursa. Sex was determined by gonadal inspection. Birds were classified as hatching-year (born during the current calendar year), subadult (born at least one calendar year previously, but not yet reproductive), or adult (physiologically capable of reproduction) using a combination of data on bursa of Fabricius (Broughton 1994), body-plumage coloration, presence or absence of flight-feather molt, culmen length (Baker 1993, C. Thompson unpubl. data), and reproductive condition, including presence or absence of an incubation patch. Molt and plumage terminology follow Humphrey and Parkes (1959). Birds with fleshy bursas, no indication of reproductive organ maturity (e.g. tiny, relatively undifferentiated gonads and associated reproductive structures such as oviducts and vas deferens), in juvenile or first basic plumage (or first prebasic molt between these plumages), lacking flight-feather molt, and with a culmen length less than 43 mm were considered to be hatching-year birds. Birds in alternate plumage, definitive basic plumage, or with flight-feather molt and that had a fleshy or thin-walled bursa, culmen length greater than 43 mm, and an immature reproductive system were considered to be subadults. Birds in alternate plumage, definitive basic plumage, or with flight-feather molt and a membranous bursa or no bursa (or rarely a thin-walled bursa), culmen length greater than 43 mm, and a mature reproductive system (e.g. large ovarian follicles and hypertrophied oviduct) were considered to be adults. In 1993, 12 adult males, 6 adult females, 6 subadult males, and no subadult females were examined. In 1996, 42 adult males, 29 adult females, 14 subadult males, and 19 subadult females were examined.

*Molt-score calculation.*—Primaries and secondaries are numbered from the innermost (P1) to outermost (P10; not including vestigial P11), and outermost (S1) to innermost (usually S16), respectively. Rectrices are numbered from the central pair (R1) to the outermost pair (R6). For nonmolting adult males ( $n = 20$ ) and females ( $n = 15$ ), the length of each of their 10 functional primaries, 16 secondaries, and 12 rectrices (Nitzsch 1840, C. Thompson unpubl. data) was measured 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, the lengths of the primaries, secondaries, and rectrices were summed to give cumulative lengths of all primaries, secondaries, and rectrices, respectively. For molting birds, all growing feathers were measured in the same fashion. Old feathers received a score of 0; empty follicles were assigned a value of 1.0 mm to indicate that the old feather was lost. As above, all values were summed to give a cumulative measure of growth. Primary-molt score for each molting bird was calculated by dividing the cumulative primary growth of a molting bird by the mean total primary length of a nonmolting bird of same sex and multiplying by 100, i.e. primary-molt score was calculated as a percentage of total regrowth, the minimum molt score being 0.01 and the maximum being 99.99. Secondary- and rectrix-molt scores were calculated in analogous fashion.

*Statistics and estimating duration of flight-feather molt.*—Statistics were conducted using SYSTAT 5.0 for windows (Wilkinson 1992). Remex and rectrix measurements were correlated within individual birds. Therefore, the relative shapes of the primaries, secondaries, and rectrices of males and females were analyzed using two-way repeated-measures ANOVA where primary, secondary, or rectrix length was one factor and sex was the other.

Most methods for estimating the duration of flight-feather molt regress date on molt score (Pimm 1976) or vice versa (Ginn and Melville 1983). These methods assume that flight-feather molt score increases linearly from onset to completion of molt. This assumption is based on the observation that flight feathers grow at a fairly constant rate regardless of their total length when fully grown (but see Ashmole 1962). How accurately these methods estimate molt duration depends on various factors but is especially influenced by the methods used to score molt. The most commonly used method for scoring molt (Newton 1966, Ginn and Melville 1983) assigns equal weight to all flight feathers. However, because short feathers begin and finish growth in less time than longer feathers, and are given as much weight as longer feathers, this scoring system causes flight-feather molt score to increase nonlinearly over the course of molt in species such as alcids and shorebirds (Ashmole 1962, Summers 1980) that have remiges that differ considerably in length. The methods we used to score flight-feather 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 methods. Our data also are especially well suited for analysis by a method developed by Underhill and Zucchini (1988) and Underhill et al. (1990) that overcomes many of the potential biases and limitations of Pimm's (1976), Newton's (1966), and other linear regression methods, and yields more accurate estimates of molt duration as a result. Unfortunately,

Underhill and his colleagues provided no mechanism (e.g. software program) to enable other researchers to employ their method without their assistance. As a result, we used Pimm's method to estimate the timing, rate, and duration of flight-feather molt.

Following Pimm (1976), collection date was used as the dependent variable and was regressed on flight-feather (primary, secondary, or rectrix) molt score. Using collection date as the dependent rather than the independent variable yields estimates of the timing, duration, and rate of molt for individual birds, which were among the goals of this paper. Reversing the axes yields estimates of the timing, duration, and rate of molt for populations of birds (Pimm 1976). In regression analyses, comparisons of time of onset and rate of flight-feather molt between ages and sexes were made using two-sample *t*-tests with separate variances of slope and y-intercept data; otherwise, Mann-Whitney-*U* tests were used when molt-score data were not significantly correlated with collection date.

RESULTS

*Wing length, tail length, and body mass.*—Adult males have significantly longer primaries, shorter secondaries, and longer rectrices than do adult females (primaries:  $F = 10.87$ ,  $df = 1$  and  $9$ ,  $P < 0.001$ ; secondaries:  $F = 7.95$ ,  $df = 1$  and  $9$ ,  $P = 0.005$ ; rectrices:  $F = 11.41$ ,  $df = 1$  and  $9$ ,  $P = 0.001$ ; Figs. 1A–C). Female primaries, secondaries, and rectrices averaged  $1,095.7 \pm SE$  of  $10.0$  mm,  $1,031.6 \pm 8.7$  mm, and  $289.6 \pm 3.0$  mm, respectively. Male primaries, secondaries, and rectrices averaged  $1,113.0 \pm 3.5$  mm,  $1,012 \pm 7.1$  mm, and  $301.4 \pm 4.4$  mm, respectively.

Both subadult and adult males are significantly heavier than females (subadults: males =  $1,050 \pm 15$  g, females =  $992 \pm 14$  g,  $t = 2.76$ ,  $df = 40$ ,  $P = 0.009$ ; adults: males =  $1,096 \pm 7$  g, females =  $990 \pm 7$  g,  $t = 3.02$ ,  $df = 198$ ,  $P < 0.001$ ).

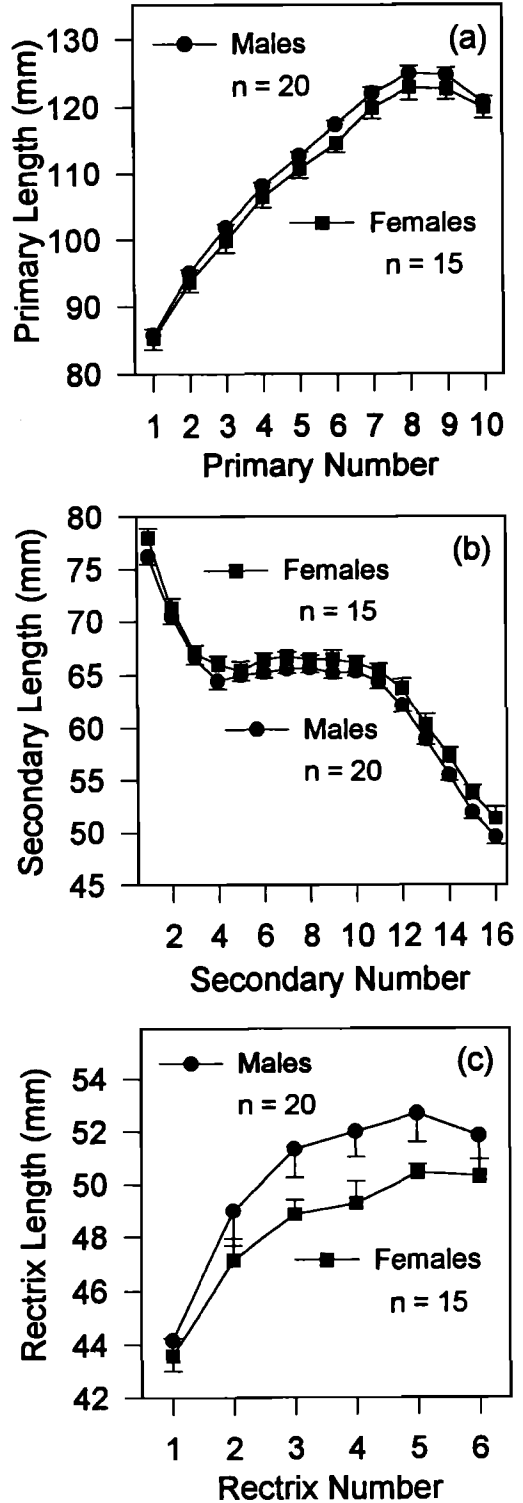


FIG. 1. (A) Primary length of adult Common Murres in relation to primary number. Primaries numbered from proximal (P1) to distal (P10). (B) Secondary length of adult Common Murres in relation to secondary number. Secondaries numbered from distal (S1) to proximal (S16). (C) Rectrix length of adult Common Murres in relation to rectrix number. Rectrices numbered from central pair (R1) to outermost pair (R6). Values are  $\bar{x} \pm SE$ .

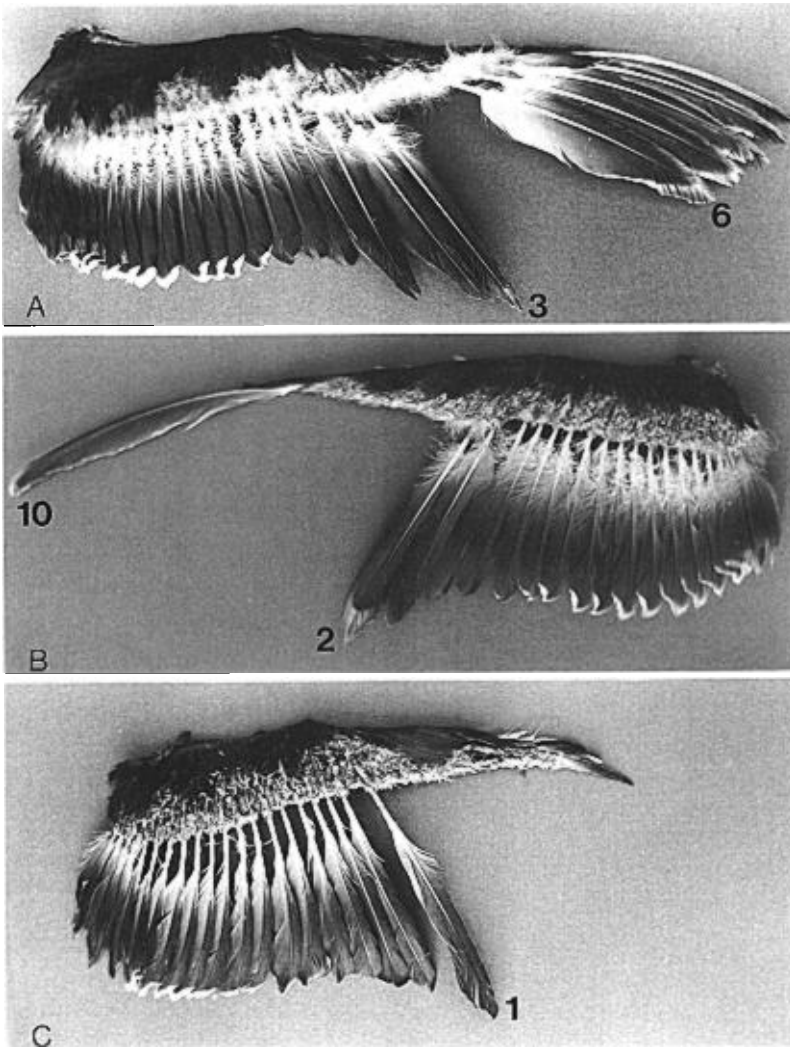


FIG. 2. (A) Molting wing of adult Common Murre missing P4 and P5; P3 and P6 indicated by numbers on the figure. (B) Molting wing of adult Common Murre missing P3 to P9; P2 and P10 indicated by numbers on the figure. (C) Molting wing of adult Common Murre missing P2 to P10; P1 indicated on the figure.

*Sequence of flight-feather loss and replacement.*—Subadult and adult Common Murres replace their flight feathers once a year in late summer or fall. Common Murres exhibit an unusual sequence of primary replacement among birds. Contrary to all published literature, primaries are not dropped synchronously. Instead, molt is initiated at a single focus in the middle of the primaries between P4 and P7 and progresses in two concurrent, rapid waves proximally to P1 and distally to P10 (Fig. 2A–C, Table 1). P1 and P2 are not lost until after P10 has been dropped (Fig. 2C, Table

1), P1 dropping after P2. The first primaries to be lost also are the first to be replaced; this is reflected by the greater length of the middle primaries relative to more proximal and distal primaries during the first one to two weeks of primary molt (Figs. 3A–B, 4).

Secondary molt is delayed until after all old primaries are lost. On average, secondary molt begins and finishes when primaries are 27 and 99% grown, respectively (Fig. 5A). Of the sample of molting birds examined, we found 35 birds that had lost some but not all primaries (Table 1, Fig. 2A–C), but only two specimens

TABLE 1. Location of missing primaries in Common Murres undergoing definitive prebasic molt.

No. missing primaries	<i>n</i> <sup>a</sup>	Location of missing primaries									
		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
1	1	0	0	0	1	0	0	0	0	0	0
2	1	0	0	0	1	1	0	0	0	0	0
3	2	0	0	0	0	2	2	2	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0
5	4	0	0	2	2	2	4	4	2	2	2
6	3	0	0	0	1	3	3	3	3	3	2
7	3	0	0	3	3	3	3	3	3	3	0
8	6	0	0	6	6	6	6	6	6	6	6
9	15	0	15	15	15	15	15	15	15	15	15
10	104	104	104	104	104	104	104	104	104	104	104

<sup>a</sup> Number of birds replacing a given number of primaries.

that had lost some but not all secondaries (Fig. 3C). Based on this, we presume that secondaries are lost more rapidly than the primaries, the innermost ones being the last to drop (Fig. 3C). Growth of new secondaries appears to begin at two foci (S1 and probably about S8), and to progress in two concurrent waves: proximally from S1 to S4, and both proximally and distally from S8. Like the primaries, this appears to be illustrated by the greater length of S1 and S8 compared with their adjacent secondaries (Fig. 3B). This growth pattern suggests that secondaries may be lost in the same sequence as well. These conclusions are tentative, however, and merit further study.

Like the remiges, old rectrices are shed rapidly; however, we could not discern any sequence of rectrix loss or regrowth. Regression of rectrix-molt score on primary-molt score indicates that, on average, rectrix molt begins when primaries are 43% grown, and is 88% completed when primary molt is finished (Fig. 5B). Similarly, regression of rectrix-molt score on secondary-molt score indicates that, on average, rectrix molt begins when secondaries are 20% grown, and is 81% completed when secondary molt is finished. Rectrix molt is completed 3 to 10 days after completion of secondary molt, and 2 to 7 days after completion of primary molt, depending on the rate of feather growth during a given molt; this can be deduced from: (1) the rate of primary growth as indicated by the regression of date on primary-molt score (Fig. 6A–B; discussed below), and (2) the rate of rectrix molt in relation to primary and secondary molt as indicated by regressions of rectrix-molt score on primary- and secondary-molt score (Fig. 5B–C).

*Timing and duration of flight-feather molt.*— Regressions of collection date on primary-molt score for adult versus subadult males in 1996 indicate that, on average, subadult males began and finished primary molt on 2 and 26 August, respectively, versus 15 August and 9 September for adult males ( $t = 4.29$ ,  $df = 53$ ,  $P < 0.001$ ; Fig. 6A–B). Given that subadult and adult males both begin and finish flight-feather about two weeks offset from one another, it is not surprising that they did not differ in their rate of primary molt ( $t = 0.02$ ,  $df = 52$ ,  $P > 0.9$ ; Fig. 6A–B); i.e. total average duration ( $\bar{x} \pm 95\%$  CI) of molt for adult and subadult males was  $24.9 \pm 22.6$  days and  $23.9 \pm 22.6$  days, respectively.

The same analyses conducted on data from males collected in 1993 indicate that, in contrast to 1996, subadult and adult males began primary molt at approximately the same time (11 and 13 August, respectively;  $t = 1.64$ ,  $df = 15$ ,  $P > 0.1$ ; Fig. 6A–B). However, like males in 1996, the rate of primary molt did not differ between subadults and adults ( $t = 0.02$ ,  $df = 14$ ,  $P > 0.9$ ; Fig. 6A–B); i.e. total average duration of molt for adult and subadult males was  $81.1 \pm 8.6$  days and  $75.4 \pm 8.1$  days, respectively. It is noteworthy, however, that primary molt in both subadult and adult males required more than three times as long to complete in 1993 than in 1996; perhaps because of small sample sizes, however, these differences were not statistically significant (adults:  $t = 1.29$ ,  $df = 49$ ,  $P > 0.2$ ; subadults:  $t = 1.30$ ,  $df = 16$ ,  $P > 0.2$ ).

Regression analyses for adult and subadult females indicate no significant relationship between primary-molt score and date in 1996

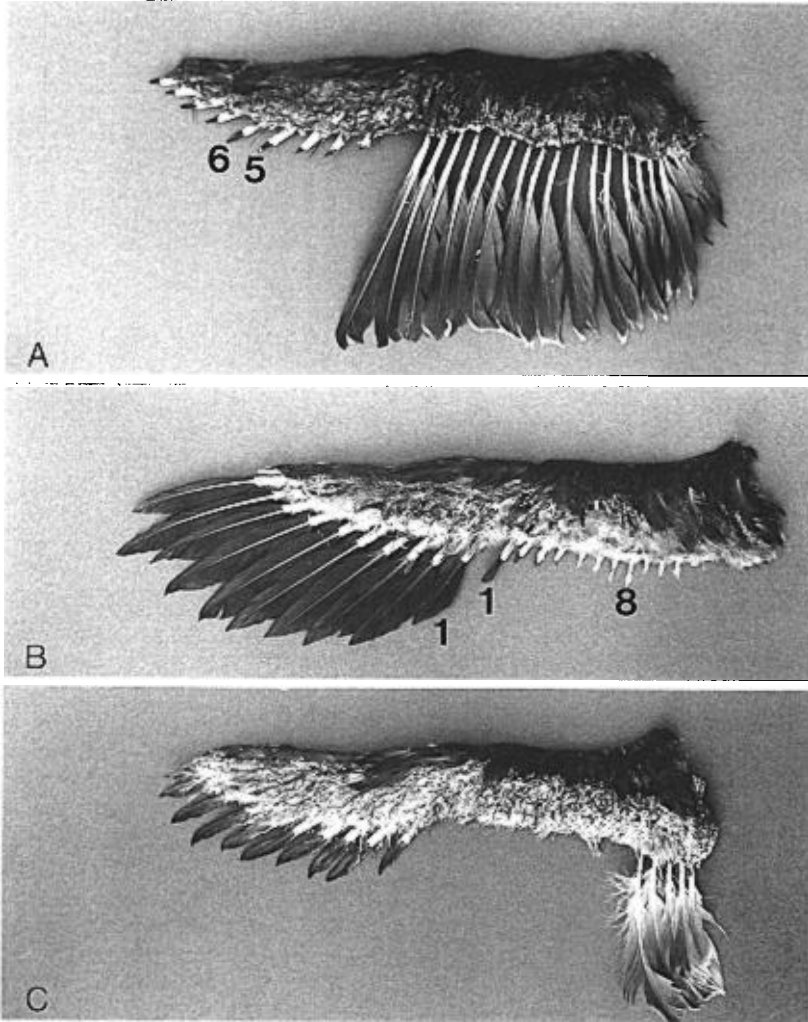


FIG. 3. (A) Molting wing of adult Common Murre growing P2 to P10; P5 and P6 indicated by numbers on the figure. (B) Molting wing of adult Common Murre. P1, S1 and S8 indicated by numbers on the figure. Note the greater lengths of the middle primaries relative to more proximal and distal primaries, and the decreasing length of the secondaries from S1 to S4, and from S8 both distally and proximally. (C) Molting wing of adult Common Murre growing P1 to P10; S1 to S11 are missing, and S12 to S16 are old.

(adult females:  $t = -0.65$ ,  $P = 0.522$ ; subadult females:  $t = 0.35$ ,  $P = 0.732$ ; Fig. 6C). However, primary-molt scores of subadult females ( $\bar{x} = 26.3 \pm 4.8$ ) were significantly higher than those of adult females ( $\bar{x} = 2.5 \pm 1.3$ ) indicating that, like males, subadult females molt earlier than adult females (Mann-Whitney  $U$ -test,  $U = 85$ ,  $df = 1$ ,  $P < 0.001$ ). Median primary-molt scores did not differ between subadult males and females ( $U = 103$ ,  $df = 1$ ,  $P = 0.274$ ) or adult males and females ( $U = 593$ ,  $df = 1$ ,  $P = 0.851$ ), suggesting that timing of molt did not differ

between sexes (within age classes) in 1996. Sample sizes of adult ( $n = 6$ ) and subadult ( $n = 0$ ) females in 1993 were too small for meaningful statistical analyses.

From the discussion above, it can be deduced that secondary and rectrix molt are completed, on average, in about 72 and 65%, respectively, of the time required for primary molt. Because the duration of primary molt varies widely among years (Fig. 6A–B), the duration of secondary and rectrix molt varies as well.

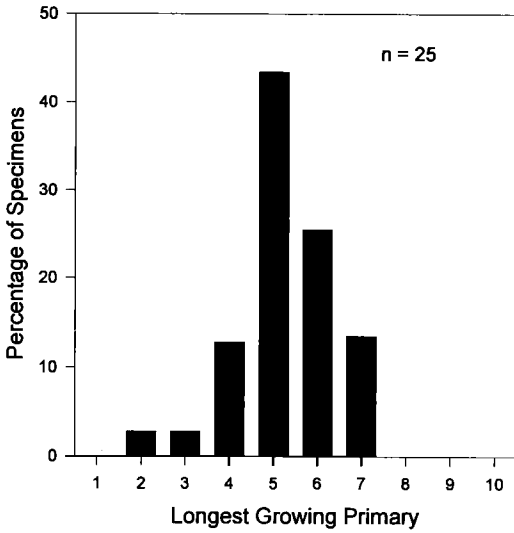


FIG. 4. Frequency of longest growing primary in 25 adult Common Murres during early stages of definitive prebasic molt. Because distal primaries grow significantly faster than proximal primaries (C. Thompson unpubl. data), data were tabulated only for specimens in which growing primaries did not exceed 30 mm in length.

DISCUSSION

Common Murres are distributed throughout temperate to arctic marine waters of the Northern Hemisphere (Cramp 1985). As a result, they exhibit extensive geographic variation in morphology, as is reflected by the seven or so subspecies that are commonly recognized (Storer 1952). Therefore, the results of our study apply to the subspecies *californica* and possibly *inornata* (AOU 1957) that we studied, but they potentially may not apply to other subspecies.

*Wing and tail shape.*—Adult males have slightly but significantly longer and narrower wings, and thus a higher aspect ratio, than adult fe-

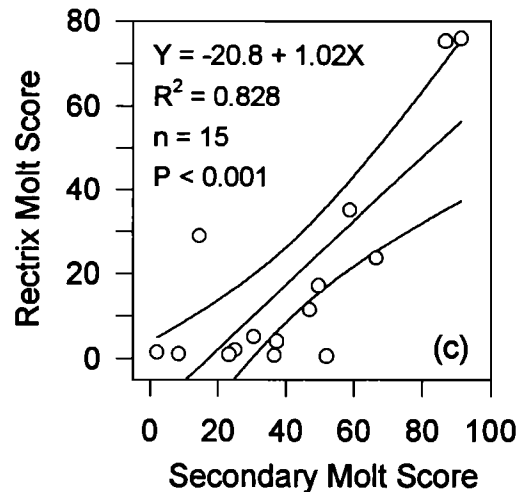
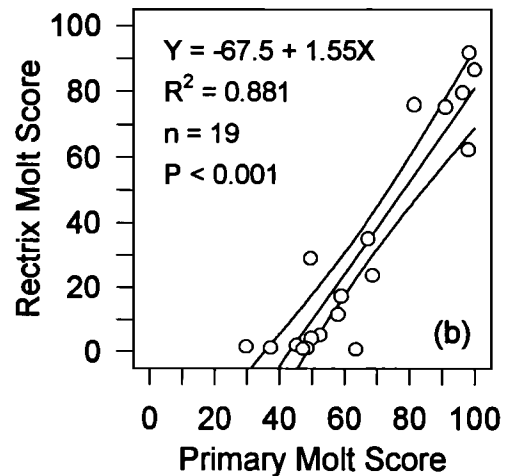
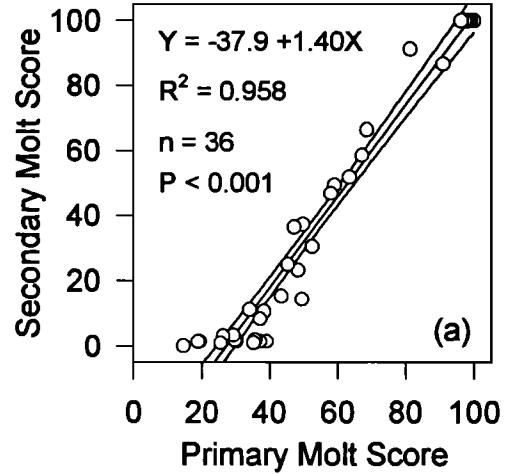


FIG. 5. (A) Regression of secondary-molt score on primary-molt score for all subadult and adult male and female Common Murres collected in 1993 and 1996 with molting primaries and secondaries. (B) Regression of rectrix-molt score on primary-molt score for all subadult and adult male and female Common Murres collected in 1993 and 1996 with molting primaries and rectrices. (C) Regression of rectrix-molt score on secondary-molt score for all subadult and adult male and female Common Murres collected in

1993 and 1996 with molting secondaries and rectrices. Regression lines are shown  $\pm 95\%$  confidence intervals.

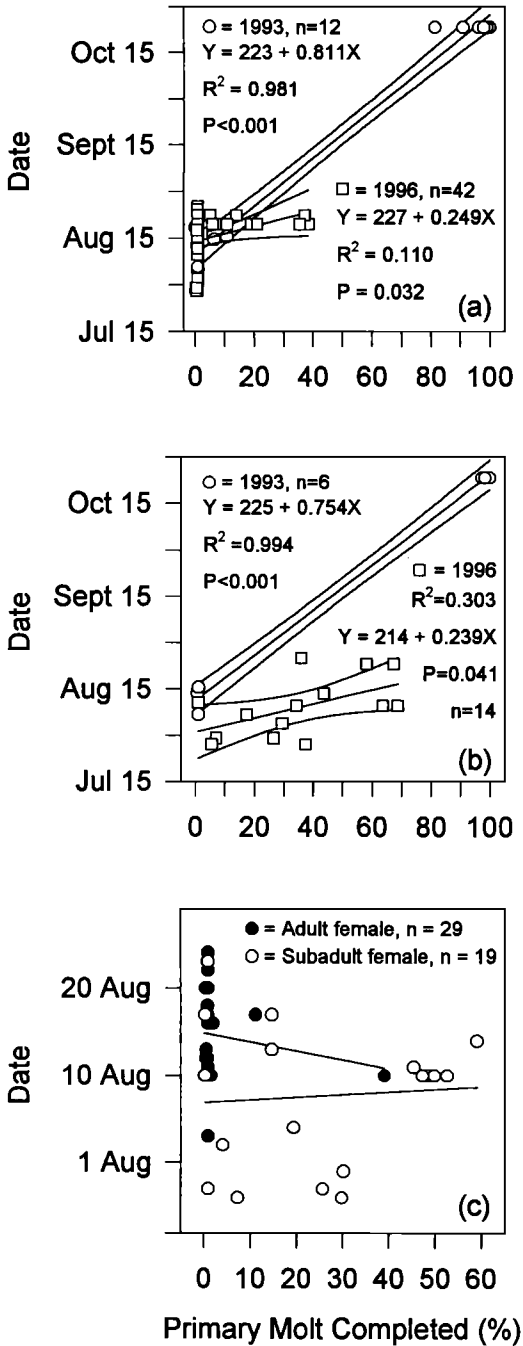


FIG. 6. (A) Regression of collection date on primary-molt score for adult male Common Murres collected in 1993 and 1996. (B) Regression of collection date on primary-molt score for subadult male Common Murres collected in 1993 and 1996. (C) Regression of collection date on primary-molt score for adult and subadult female Common Murres collected in 1996. Regression lines in A and B are shown  $\pm 95\%$  confidence intervals.

males. To our knowledge, such a difference is not known within a single population of any species that is relatively monomorphic in body size, but it has been described between sexes in raptors that are sexually size dimorphic (Mueller et al. 1981), and in migratory versus nonmigratory populations of various passerines (e.g. Berthold and Querner 1982, Chandler and Mulvihill 1988). The only potential adaptive significance that we are aware of that may explain the difference in wing shape between male and female murres relates to differences in body mass. Among different populations of Common Murres, no consistent dimorphism in wing length or body mass exists between males and females. Males are slightly heavier and/or longer-winged in some populations and slightly smaller and/or shorter-winged in others (Cramp 1985, Harris and Wanless 1988). However, in our study population, both subadult and adult males are significantly heavier than females. Among species of Procellariiformes, aspect ratio, and thus flight efficiency, increases with increasing body mass (Warham 1977). In the population of Common Murres that we studied, males may have a higher aspect ratio than females in order to increase their flight efficiency, thereby compensating for their greater body mass.

*Flight-feather molt.*—Primary molt begins at a single focus between P4 and P7, and progresses in two rapid waves proximally to P1 and distally to P10. Contrary to our results, Birkhead and Taylor (1977) noted one Common Murre that dropped P10 first and another that dropped P9 and P10 first. This unusual sequence of flight-feather molt, termed "Hampe's Rule" by Stresemann and Stresemann (1966: 356) based on work by H. Hampe, is shared by all parrots (Forshaw and Cooper 1989), all members of the Falconidae (Stresemann and Stresemann 1960, 1966), and one species of kingfisher (Pied Kingfisher [*Ceryle rudis*]; Cramp 1985). This molt sequence also has been reported in certain hummingbirds (Wagner 1955). However, subsequent studies of many of the species that Wagner studied suggest that Wagner's data are incorrect, perhaps because of methodological errors (Russell et al. 1994, Scott 1994, Stiles 1995). That this molt strategy exists in such phylogenetically unrelated and ecologically disparate groups as alcids, falcons, parrots, and kingfishers indicates that it evolved



independently in each of these lineages. In addition, given the different natural histories and morphologies (e.g. wing shapes) of these groups, the adaptive significance of this molt strategy is unclear.

Previous authors have stated that Common Murres shed their primaries nearly simultaneously, e.g. "synchronously" (Stresemann and Stresemann 1966), "simultaneously" (Taverner 1929, Witherby et al. 1941, Salomonsen 1944, Tuck 1960, Croll 1990), "all shed at one time" (Storer 1952), "almost simultaneously" (Ginn and Melville 1983), "almost all at once" (Dement'ev and Gladkov 1951), "within one to three days" (Cramp 1985), and "within a few days of each other," based on captive birds (Birkhead and Taylor 1977).

Secondary molt begins and finishes when primaries are about 38 and 99% grown, respectively (see Birkhead and Taylor 1977). New secondaries appear to be lost and regrown beginning at two foci (S1 and probably S8) and progressing in two concurrent waves: proximally from S1 to S4, and proximally and distally from S8. As with primary molt, all previous sources state that secondaries are lost and regrown "simultaneously" (e.g. Birkhead and Taylor 1977). Regarding the timing of secondary molt relative to primary molt, previous sources vary from stating that secondaries are dropped at the same time, or nearly so, as the primaries (Salomonsen 1944, Dement'ev and Gladkov 1951, Storer 1952, Tuck 1960) to when the primaries are "almost half grown" (Birkhead and Taylor 1977), or after the primaries have dropped (Witherby et al. 1941).

Rectrices are lost very rapidly and in no discernible order, as found by Birkhead and Taylor (1977) and Storer (1952). On average, the rectrices begin to regrow when the primaries and secondaries are 43 and 20% grown, respectively, but at the completion of primary and secondary molt, they are only 88 and 81% grown. Previous authors have stated that rectrices are dropped "simultaneously" with the primaries (Tuck 1960), "shortly after primaries have begun to regrow" (Storer 1952), "simultaneously" with the secondaries (Witherby et al. 1941), when the primaries are "about half grown" (Birkhead and Taylor 1977), when the primaries are "less than 120 mm" (a little more than half grown; Salomonsen 1944), or "later" than the primaries (Kozlova 1957). We found

that the rectrices complete regrowth two to seven days after primary molt is complete. In contrast, Birkhead and Taylor (1977) estimated that rectrix molt was not finished until 30 days after completion of primary molt.

*Calendar timing.*—Flight-feather molt in both 1993 and 1996 began in early to mid-August. However, because this molt took more than three times as long to complete in 1993 than in 1996, molt finished in late August to mid-September in 1996 versus late October to early November in 1993. Elsewhere, flight-feather molt has been reported to occur in late July or early August through mid- to late September (Forbush 1925, Dement'ev and Gladkov 1951, Cramp 1985, Hope Jones and Rees 1985, Harris and Wanless 1990), July to early or late November (Verwey 1924, Witherby et al. 1941, Salomonsen 1944), September and October (Dement'ev and Gladkov 1951, Kozlova 1957), and "beginning sometimes in August but often not until September," its ending date unspecified (Bent 1919). Some of the variation among these dates reflects the fact that northern populations molt later, on average, than more southerly populations (Cramp 1985), and that young subadults as well as older adult nonbreeders and failed breeders begin and finish molt earlier than successful breeders (Verwey 1924, Birkhead and Taylor 1977, Swennen 1977, Hope Jones and Rees 1985, Harris and Wanless 1990).

*Age and sex differences.*—As found in many other seabirds (e.g. Palmer 1962, Cramp 1977, 1983, 1985, Warham 1996), we found that subadult Common Murres molt earlier than adults. Swennen (1977) reported the same results regarding a captive population of Common Murres. Because subadults do not breed or care for young, they are able to molt earlier than adults, especially adults that breed successfully.

We detected no difference in timing of molt between sexes within age classes. Primary-molt score was significantly correlated with Julian date in both adult and subadult males but not in adult or subadult females (Fig. 6A and 6B vs. 6C). The reason for this is unclear. Anecdotal evidence suggests that males molt either earlier or later than females in other populations (Hope Jones and Rees 1985, Tasker et al. 1987). Common Murre chicks fledge at about 21 to 26 days of age before their primaries have begun to grow. As a result, they are accompa-

nied at sea and provided food by their fathers until they are capable of flight at about 100 days of age, and possible longer (Birkhead 1984, 1993; Hope Jones and Rees 1985). For a few weeks after their young have left the colony, females continue to return to the breeding colony (Varoujean et al. 1979, Wanless and Harris 1986). Depending on the rate of molt in a given year, Common Murres are thought to be flightless for 45 to 60 days during molt (Glutz von Blotzheim and Bauer 1982). As a result, rather than delaying molt until they are finished caring for their young, one might expect successful breeding males to molt earlier than their mates because they may be constrained to doing little or no flying while accompanying their flightless young at sea. Alternatively, because females are emancipated from parental duties after their young go to sea, they may be able to begin molting as soon as they leave the breeding colony, whereas the continued parental duties of males may preclude them from beginning molt until their young are more self sufficient.

*Molt duration.*—Duration of flight-feather molt appears to be remarkably variable. In both subadult and adult males in 1996, primary molt required 24 to 25 days, whereas in 1993 it required 75 to 81 days, on average. Adult murres entangled in Puget Sound in the fall are comprised of postbreeders from both Oregon and Washington. Postbreeding murres from Oregon molt about four to six weeks earlier than those from Washington. Thus, between-year differences in molt duration in adults could be due to different proportions of postbreeding Oregon versus Washington murres. However, because nonbreeding subadult males showed nearly identical between-year differences in molt duration, this possibility is unlikely.

On average, secondary and rectrix molt require 72 and 65% as much time as primary molt. Based on quantitative analyses similar to ours, Birkhead and Taylor (1977) estimated the duration of primary, secondary, and rectrix molt to be  $62.7 \pm 16.3$  days,  $25.0 \pm 8.4$  days, and  $61.0 \pm 16.8$  days, respectively, giving a total flight-feather molt duration of about 93 days, on average. Similarly, Glutz von Blotzheim and Bauer (1982) stated the duration of primary, secondary and rectrix molt to be 42 to 90 days, 25 days, and 35 to 86 days, respectively, although the source(s) of these data is unclear.

Other less-quantitative estimates of flight-feather molt duration include "about 60 days" (Ginn and Melville 1983) and "less than 70 days" (Harris and Wanless 1990).

*Evolutionary implications.*—The unusual sequence of replacement of primaries in Common Murres raises the intriguing question: Why does their primary molt begin at a central focus in the middle of the primaries and progress in two concurrent waves? Because murres lose all of their primaries within a few days, it is difficult to imagine that the unusual sequence by which they lose them is more advantageous than the more typical "synchronous" or rapid primary replacement of other large alcids and diving seabirds (e.g. May 1930, Palmer 1962, Stresemann and Stresemann 1966, Watson 1968, Bellrose 1980, Piersma 1988, Warham 1996). The most likely *a priori* explanation for the primary-molt sequence in Common Murres is that it reflects their phylogenetic history, i.e. that an ancestor exhibited the same molt sequence for reasons unknown.

Common Murres are most closely related to Thick-billed Murres (*Uria lomvia*), Razorbills (*Alca torda*), Dovekies (*Alle alle*), and Great Auks (*Pinguinus impennis*; Strauch 1985, Friesen et al. 1993, Moum et al. 1994; contra Chandler 1990). Like the literature on Common Murres, that on Thick-billed Murres, Razorbills, and Dovekies states that they molt their flight feathers synchronously (Taverner 1929, Salomonsen 1944, Dement'ev and Gladkov 1951, Stresemann and Stresemann 1966, Bradstreet 1982, Bédard 1985, Cramp 1985, Hope Jones and Rees 1985, Harris and Wanless 1990). However, the one and only known molting specimen of Great Auk (Grieve 1885, Meldgaard 1988) appears to indicate that primary molt began in the middle of the primaries as in Common Murres. This specimen has "on the right wing, a pin feather. . .near the middle of the series of primaries; and on the left wing, one primary [P4 or P5] appears new whereas the rest of the primaries are faded and badly worn" (Storer 1960). Finn Salomonsen made similar comments about this specimen to the Stresemanns (Stresemann and Stresemann 1966). This indicates that Great Auks molted their primaries slowly. In addition, we speculate that they molted their primaries sequentially, presumably in the same or similar order as Common Murres (Salomonsen 1945, Storer 1960, Stresemann and Stresemann

1966). In addition, in the absence of specimens from which this could be deduced empirically, simple physical principles suggest that this must have been the case.

The wing size and shape of volant alcids are a compromise between selection pressures for flying in the air and swimming underwater. Therefore, the wing is not optimally designed for either function. As a result, compared with non-diving seabirds of comparable body sizes (Warham 1977), alcids have relatively high wing loading, ranging from less than 1.5 g per cm<sup>2</sup> of wing area for most small alcids up to about 2 g per cm<sup>2</sup> for large alcids, including Common Murres (Livezey 1988). Because Great Auks were flightless, their wings were more optimally adapted for flight underwater. Thus, like penguins, their wing area was small relative to their body size, resulting in very high wing loading, estimated to have been about 22 g per cm<sup>2</sup> of wing area, more than 10 times the maximum wing-loading exhibited by Common Murres (Livezey 1988). Similarly, the ratio of their wing area to cross-sectional body area also was very high. If Great Auks lost all of their primaries rapidly like large volant alcids, they would not have had sufficient wing area remaining to propel themselves fast enough underwater to obtain food and, perhaps, to escape predators. Therefore, they must have replaced their primaries slowly and sequentially. This raises another question that we will not address, but that is worth pondering: Why did Great Auks molt their flight feathers in two slow and concurrent sequential waves progressing proximally and distally from a focus in the middle of the primaries, rather than in a single wave or possibly two waves from two foci?

Returning to our original question: Why do Common Murres replace their primaries in two concurrent waves from a single focus in the middle of the primaries? Unfortunately, there is no obvious answer to this question. *Uria* appears to have evolved before *Pinguinus*. Thus, the presumed slow molt of Great Auks probably is a derived character, whereas the two concurrent waves of molt likely may be a shared-derived character of the clade to which *Alle*, *Uria*, *Alca*, and *Pinguinus* belong, and possibly of other alcids as well (Braune 1987). The only selective advantage that we can think of is that this molt strategy may allow these alcids to

drop and regrow their primaries more rapidly than by dropping and regrowing them in a single wave, as has been argued for other species in which the long duration of molt may interfere with other energetically demanding periods in the annual cycle (e.g. Langston and Rohwer 1996).

These conclusions raise two additional interesting questions. First, do Thick-billed Murres, Razorbills, and Dovekies molt their primaries synchronously as the literature suggests? We speculate that they do not. The molt sequence in Common Murres was overlooked by previous researchers for many obvious reasons: (1) during molt, individual birds lose all of their primaries very rapidly, probably within a few days; thus, depending on the synchrony of molt within a population, a large number of specimens must be examined within a narrow window of time to detect the sequence of loss of primaries; (2) like other large alcids, they molt at sea where it is more difficult to collect birds than on a breeding colony; (3) molting specimens are more difficult to prepare and less aesthetically attractive as study skins than are nonmolting birds; thus, historically and even currently, specimen preparators have preferred not to prepare molting specimens; (4) for the two preceding reasons, relatively few molting specimens are in museums; and (5) because nearly all study skins are prepared as "round" skins with both wings folded, examining remiges for molt is difficult or impossible without damaging specimens. Thus, we suggest that Thick-billed Murres, Razorbills, and Dovekies molt in the same sequence as Common Murres and Great Auks. Given the tens of thousands of alcids killed in commercial fisheries each year in both the North Atlantic and North Pacific during their molting seasons, obtaining specimens to answer this question should be relatively easy (King 1984, Ogi 1984, Piatt and Nettleship 1987, DeGange et al. 1993). Alternatively, observations of captive alcids in zoos and aquaria also could help answer this question (Douma and Carlson 1994, Gunther 1994).

The second question is why do Dovekies lose their primaries rapidly? Other than the Whiskered Auklet (*Aethia pygmaea*) and Least Auklet (*A. pusilla*), Dovekies are the smallest in mass of the 23 extant alcids (Bent 1919, Johnson 1944, Cramp 1985). All other small- to medium-size alcids (*Aethia*, *Ptychoramphus*, *Cyclorhynchus*,

and *Brachyramphus*) replace their primaries sequentially and more slowly than larger alcids (Payne 1965; Bédard and Sealy 1984; Emslie et al. 1990; Byrd and Williams 1993; Manuwal and Thoresen 1993; Carter and Stein 1995; Konyukhov and Kitaysky 1995; Jones 1993a, b; Nelson 1997), whereas larger alcids (*Synthliboramphus*, *Cerorhinca*, *Cephus*, *Alca*, and *Fratercula*) replace their primaries much more rapidly (Harris and Yule 1977, Ewins 1988, 1993, Drost and Lewis 1995, Gaston and Dechesne 1996). Like our discussion of wing loading above, simple physical principles and allometric considerations explain why primaries should be molted slowly in small alcids and rapidly in large alcids. The explanation for this general difference between small and large alcids ostensibly lies in understanding what determines optimal wing size for aerial versus underwater flight. Optimal wing area for aerial flight is dictated by wing loading. In contrast, for underwater flight, optimal wing area is dictated by the ratio of the cross-sectional area of a bird's body divided by the surface area of its partly folded wings (the partly folded wings during underwater flight increase structural support of the wing). If large alcids have the same proportions as small alcids, then as linear body measures (body diameter and wing length) increase from small to large species, body volume (mass) should increase with the cube, whereas body cross-sectional area and wing area should increase with the square. In addition, wing area should increase with body mass to the 0.667 power, resulting in increasing wing loading with increasing body mass (Storer 1960, Greenwalt 1962, 1975). Thus, for a large alcid to maintain the same aerial flight ability as a small alcid, it would need to maintain the same wing loading (or increase wing power, i.e. increase wingbeat frequency). To do so, wing-surface area would have to increase with the cube, rather than the square, of body mass, i.e. wing area would have to increase with body mass to the 1.0 power, rather than to the 0.667 power. In fact, however, empirical data indicate that wing area of extant alcids scales to 0.588 (Warham 1977) to  $0.632 \pm 0.003$  (Livezey 1988); both empirically derived exponents are statistically significantly less than the power of 0.667 predicted by the law of isometry described above (Warham 1977, Livezey 1988). Thus,

large alcids have much higher wing loading than small alcids.

In contrast, for a large alcid to maintain the same underwater flight ability as a small alcid, it would need to maintain the same ratio of wing-surface area to body cross-sectional area. Because wing-surface area and body cross-sectional area both scale with the square of linear body measurements, this ratio is maintained by allometry alone. Thus, as body mass increases, selection favors relatively larger wings for aerial versus underwater flight such that the difference between the wing sizes that are optimal for each "flight" mode also increases. In short, this means that the wings of small alcids are nearly optimal in size for aerial flight when fully extended and also for underwater flight when partially folded, whereas the wings of large alcids are smaller than optimal for aerial flight and larger than optimal for underwater flight. The supposed consequence of this for molt in small alcids is that if they lose all of their primaries rapidly, their wing-surface area will be reduced so far below what is optimal for underwater flight that their ability to fly underwater is seriously compromised. In addition, as in large alcids, rapid loss of primaries would make aerial flight impossible for most of the molting period until the new primaries are about 80% grown (Birkhead and Taylor 1977). As a result, most small alcids replace their primaries (and other flight feathers) slowly, thereby maintaining efficient underwater flight ability and also retaining their power of aerial flight throughout molt. In contrast, large alcids have such high wing loading that even a slow, sequential flight-feather molt would increase their wing loading sufficiently to preclude aerial flight during molt (Meunier 1951). In addition, rapid loss of all of their primaries reduces their wing-surface area to a size that is probably close to the optimal size for underwater flight. Thus, all large alcids lose their primaries very rapidly.

The question remains, why do Dovekies lose their primaries rapidly? As mentioned above, they have the third lightest body mass of any alcid. With the possible exception of Least Aukslets (Livezey 1988), they also have the lowest wing loading of any alcid (0.54 to 0.94 g/cm<sup>2</sup>; Magnan 1922, Poole 1938, Livezey 1988), yet many other relatively small alcids that have considerably higher wing loading (1.02 to 1.32

g/cm<sup>2</sup>) molt their remiges sequentially and relatively slowly. In light of the physical principles discussed above, the Dovekie's synchronous molt appears to be a curious paradox. However, we suggest a possible explanation.

The arguments discussed above are based entirely on theory; more importantly, perhaps, they implicitly assume that selection favors maintaining aerial flight ability throughout flight-feather molt in all alcid species that are sufficiently small to be physically capable of doing so. We question this assumption and argue that selection may favor flight-feather molt to be rapid and nearly synchronous rather than slow and sequential in Dovekies because, unlike any other small alcid, in the fall adults and young of all populations of Dovekies undergo long-distance migration to more southerly wintering areas (Bent 1919, Dement'ev and Gladkov 1951, Salomonsen 1950, Kozlova 1957, Bédard 1985, Cramp 1985). As a consequence, Dovekies must molt before, during, or after migration. Like most other birds, Dovekies do not undergo flight-feather molt during migration or on their wintering grounds. Instead, they molt on their breeding grounds, presumably because the cost of doing so is less than that of molting at other times, possibly because of greater food availability and/or lower predation risk on the breeding grounds. As a result, however, they are constrained to complete their flight-feather molt within a relatively short period of time. As a consequence, a slow sequential molt of flight feathers is not possible because it would require too much time. For example, Least Auklets, the ecological equivalent of Dovekies in the Pacific Ocean (Jones 1993b), require at least three months to complete their flight-feather molt (Bédard and Sealy 1984). Similarly, nonbreeding subadult Cassin's Auklets (*Ptychoramphus aleuticus*) require an average of 146 days to finish flight-feather molt (Emslie et al. 1990). As a result, Dovekies must molt their flight feathers nearly simultaneously like large alcids in order to complete their flight-feather molt before they begin fall migration.

*Correlates with prey abundance.*—El Niño conditions prevailed along the entire West Coast of North America in 1993, resulting in low food availability and nearly complete reproductive failure by murres (R. Lowe and J. Parrish unpubl. data). In contrast, food supply was abun-

dant in 1996 (J. Parrish unpubl. data). Male Common Murres molted three times faster in 1996 than in 1993. Such dramatic interyear variation in molt rate is virtually unknown in birds. In addition, subadult males molted two weeks earlier than adult males in 1996, but not in 1993. Although speculative, we suggest that these differences in molt reflect differences in prey availability between years.

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