AGE DETERMINATION AND MOLT STRATEGIES IN NORTH AMERICAN ALCIDS

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SUMMARY

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I examined 3442 specimens and measured the width of the premaxillary process at the gape ("gape width") in 2245 specimens to determine age and to trace molt patterns in 20 species of North American alcids during the first, second and definitive cycles. Gape width became significantly wider with age in specimens of all 20 species; 95% confidence intervals are presented as a preliminary guide to help age carcasses and live alcids in the hand. In order to trace presumed homologous molts across alcid taxa, results on molt are presented using standardized nomenclature. Terminology for first prebasic molts relative to the natal grounds in murres, razorbills and *Synthliboramphus* murrelets are proposed, nomenclature for the divergent molts of puffins are clarified and ornamental plumes in certain murrelets and auklets are considered basic rather than "breeding" or alternate feathers. Guidelines are presented for the sampling of up to three generations of feathers from a single individual in studies using stable isotopes, and in turn, the use of isotopes to study molt patterns is encouraged. I suggest that ancestral alcids exhibited a Complex Alternate Strategy (as do many other Charadriiformes) and that, over time, inserted molts have been lost or merged in certain species because of physical and environmental constraints.

Key words: Alcidae, gape width, sampling guidelines, molt terminology, museum specimens

INTRODUCTION

Age determination and an understanding of molt patterns in seabirds are critical components for studies on population dynamics (e.g. Ainley & Boekelheide 1990) and analyses using stable isotopes (e.g. Becker & Beissinger 2006, Moody & Hobson 2007). Determining first-year from adult seabirds picked up in oil spills or as beachcast carcasses can help to delineate age-specific dispersal patterns and the effect of spills or other mortality events on seabird populations. Understanding the timing and localities of molts can assist researchers using stable isotopes to assess distributional patterns and diet during different phases of a seabird's annual cycle. Yet because most seabirds molt at sea and usually remain away from breeding colonies until two years of age or older, the understanding of molt patterns and the ability to determine age during a seabird's prebreeding cycles remain underdeveloped. This situation is especially true of alcids, because of their at-times remote non-breeding distributions and the challenges inherent in studying them at sea (Nettleship 1996, Gaston & Jones 1998, Howell & Pyle 2005).

While examining specimens to determine age and sex in seabirds (Pyle 2008), I discovered a promising new criterion for distinguishing age classes of alcid specimens, carcasses and live birds in the hand, based on the width of the premaxillary process of the bill at the proximal end of the gape. Combining this measure with patterns of feather color and wear, I traced occurrence and extent of molts from the first through the definitive cycles. Here, I present data on the width of the premaxillary process at the gape (hereafter "gape width") and summarize molt strategies for 20 species (among 10 genera) of North American alcids. I use standardized molt and plumage nomenclature to present presumed homologous molts across alcid taxa showing diverse molting strategies. I also provide guidelines on plumage generations and molting locations to ornithologists interested in sampling feathers for isotopic analyses.

METHODS

I examined 3442 specimens of alcids at five museum collections (see "Acknowledgements"), representing most or all available skins in the collections. For each specimen, age at collection was determined based on a synthesis of plumage-aspect characters, shape and wear of outer primaries, molt limits, bill color and dimensions, and other published characteristics (Ridgway 1919, Salomonsen 1944, Dement'ev & Gladkov 1951, Kozlova 1957, Bédard & Sealy 1984, Cramp & Simmons 1985, Nettleship & Birkhead 1985, Flint & Golovkin 1990, Poole & Gill 1993–2002, Gaston & Jones 1998, and species-specific papers summarized by Pyle 2008). Age was categorized into three groups based on molt cycles (as later described):

- First cycle (typically 0–11 months old)
- Second cycle (typically 12–23 months old)
- Definitive cycle (older than first or second cycle)

Second-cycle individuals could be reliably identified for five of the 20 species (Table 1); for these, definitive cycle equated to 24 months of age or older. For the remaining 15 species, definitive cycle equated to 12 months of age or older.

I attempted to determine the age of murres and other species by the width of the supraorbital ridge (Gaston 1984, Nevins & Carter 2003), but was unable to obtain accurate data because of variation in specimen preparation techniques and difficulty in obtaining this measurement without damaging the skins. This measure is also difficult to perform on carcasses without removing the skin and musculature above the eye (Nevins & Carter 2003), and it thus cannot be obtained without harming live birds. Based on Figure 1 in Gaston (1984), however, it appeared that the width of the premaxillary process at the base of the bill might also vary by age, presumably undergoing the same ossification processes that affect the supraorbital ridge. Obtaining this measurement with dial calipers is straightforward on specimens and live birds (Fig. 1). Therefore, to investigate its use in age determinations, I measured gape width on 2425 specimens, up to 100 for each identifiable age category per alcid species. Data were excluded for specimens with visibly broken bills or with obvious irregularities in the base of the bill caused by deformity or preparation technique. Because bill dimensions in alcids may vary by sex (e.g. Nelson 1981) and by season as related to growth and shedding of ornamental bill appendages or plates in adults of some species (Stejneger 1885, Kozlova 1957), I also considered sex (as recorded on specimen labels) for all age groups and seasons for definitive-cycle alcids. Based on shedding and re-growth of ornamental bill features in several species, data was divided into non-breeding (birds collected in September–February) and breeding (birds collected in March-August) seasons.

It was impossible to completely avoid circularity between gape-width measurements and previously determined age categorization. For example, gape width caused me to re-evaluate age in some instances. However, the proportion of instances in which this re-evaluation occurred was small (estimated at < 3%), and in all cases, final age categorization was based on unbiased interpretation of criteria other than width at gape.

For each specimen, I assessed length of flight feathers and lifted contour feathers to examine for the presence of pin or developing feathers to determine whether the bird was in active molt when collected (*cf.* Pyle 2005, 2007). For specimens not molting at the time of collection (96% of all specimens examined), I carefully analyzed body feathers for contrasts in wear indicating occurrence and extents of partial molts within each cycle.

Molt terminology follows that of Humphrey & Parkes (1959) as modified by Howell *et al.* (2003). In alcids, this (hereafter "H-P") terminology includes identifiable first, sometimes second (see

TABLE 1
Width of the bill (mm) at the premaxillary process (Fig. 1) in 20 species of North American alcids

Species		First-cycle [range [a] (sample)]	Second-cycle [range [a] (sample)]	Definitive cycle [range [a] (sample)]
Dovekie	*Alle alle*	10.4–12.7 (n=16)	—	11.6–13.8 (n=57)
Common Murre	*Uria aalge*	15.1–20.8 (n=100)	—	19.6–23.8 (n=100)
Thick-billed Murre	*Uria lomvia*	16.0–21.3 (n=33)	—	20.4–24.3 (n=94)
Razorbill	*Alca torda*	15.6–19.4 (n=17)	18.7–23.6 (n=14)	22.2–27.7[b] (n=63)
Black Guillemot	*Cepphus grille*	13.0–14.7 (n=22)	—	13.9–15.5 (n=81)
Pigeon Guillemot	*Cepphus columba*	12.7–14.3 (n=100)	—	13.8–15.1 (n=100)
Marbled Murrelet	*Brachyramphus marmoratus*	8.7–12.5 (n=78)	—	11.5–13.4 (n=100)
Kittlitz's Murrelet	*Brachyramphus brevirostris*	9.6–12.4 (n=9)	—	11.8–13.8 (n=41)
Xantus's Murrelet	*Synthliboramphus hypoleucus*	8.5–10.3 (n=19)	—	9.7–11.1 (n=100)
Craveri's Murrelet	*Synthliboramphus craveri*	8.2–9.9 (n=17)	—	9.1–10.4 (n=68)
Ancient Murrelet	*Synthliboramphus antiquus*	7.7–9.9 (n=40)	—	9.0–11.2 (n=100)
Cassin's Auklet	*Ptychoramphus aleuticus*	9.3–11.2[b] (n=83)	—	10.6–12.2[b] (n=100)
Parakeet Auklet	*Aethia psittacula*	10.4–12.6 (n=21)	—	11.8–14.7[b] (n=53)
Least Auklet	*Aethia pusilla*	7.2–8.5 (n=28)	—	8.1–9.8 (n=100)
Whiskered Auklet	*Aethia pygmaea*	6.2–7.6 (n=13)	—	7.0–8.7 (n=22)
Crested Auklet	*Aethia cristatella*	9.1–12.6 (n=19)	—	12.0–16.3[b] (n=51)
Rhinoceros Auklet	*Cerorhinca monocerata*	11.1–13.9 (n=71)	13.0–16.2[b] (n=26)	14.9–18.5[b] (n=100)
Atlantic Puffin	*Fratercula arctica*	9.8–12.6 (n=16)	11.4–16.1	15.2–19.1 (n=51)
Horned Puffin	*Fratercula corniculata*	9.7–12.7 (n=26)	12.1–16.3 (n=20)	15.5–19.5[b] (n=97)
Tufted Puffin	*Fratercula cirrhata*	14.1–17.8 (n=32)	16.3–21.9 (n=17)	19.6–26.4[b] (n=100)

[a] Range (95% confidence interval) is represented by mean + SD * 1.96; thus, birds should be reliably aged if they fall outside of ranges for other age groups (see Pyle 2008).

[b] Significant sex-specific effect ($\male > \female$).

earlier discussion and Table 1), and definitive basic molt cycles, which extend between complete prebasic molts (Fig. 2). The first prebasic molt (often called the "pre-juvenile molt") is that in which the first generation of pennaceous (non-downy) feathers are grown—at the natal site in most alcids, but partially or completely at sea in murres, Razorbill *Alca torda* and *Synthliboramphus* murrelets (Fig. 2). These feathers are called "juvenal" here, reflecting wide previous usage. The complete second prebasic molt occurs at approximately one year of age at sea, and the complete definitive prebasic molts (often called "post-breeding molts") occur in older individuals, usually after breeding in adults (Fig. 2).

Basic molt cycles in birds presumably reflect ancestral molt strategies (Howell *et al.* 2003), whereas inserted molts, usually partial in extent, have evolved based on the need to replace feathers relative to environmental and physiologic constraints experienced during a species' annual cycle. In alcids, inserted molts may or may not include the preformative molt during the first cycle (traditionally called the "post-juvenile molt") and prealternate molts (traditionally called "prebreeding molts") during the first and definitive cycles. The designation of inserted molts (e.g. preformative vs. first prealternate when a single molt occurs during the first cycle) depends on how the molt was gained or other molts lost during evolution from ancestral species (Pyle 2007, 2008). Primaries are numbered distally, from the innermost (p1) to the outermost (p10).

RESULTS

Age determination in alcids by gape-width measures

Table 1 presents results of gape-width measurements, in the form of 95% confidence intervals (*cf.* Pyle 2008). In first-cycle alcids, gape widths were significantly smaller than those in definitive-cycle individuals in all 15 species that lacked an identifiable second-cycle age group (one-way ANOVAs: all $F > 8.1$, $P < 0.005$; see Table 1 for sample sizes). In all comparisons involving the five species for which second-cycle individuals could be identified, gape widths were also significantly smaller in first-cycle than in second-cycle alcids and significantly smaller in second-cycle than in definitive-cycle alcids (ANOVAs: $F > 5.8$, $P < 0.01$).

Fig. 1. Measuring the width of the premaxillary process at the proximal end of the gape ("gape width") in alcids. Calipers are positioned at the proximal end of the gape line and at a 90-degree angle to the axis of the head.

Mean gape widths of males were larger than those of females in 43 of 45 species/age groups, being slightly and nonsignificantly smaller in males than in females in first-cycle Craveri's Murrelets *S. craveri* and Whiskered Auklets *Aethia pygmaea* (ANOVAs: $F < 0.4$, $P > 0.6$). Small sample sizes, mis-sexed specimens, or both (*cf.* Parkes 1989) may have affected the latter comparisons. Males had significantly wider bills than did females (ANOVAs: $F > 4.3$, $P < 0.05$) in nine of the 45 comparisons (Table 1), most of which involved species with documented sex-specific differences in bill dimensions or those that acquire sex-specific ornamental bill features (Kozlova 1957, Nelson 1981, Cramp & Simmons 1985, Gaston & Jones 1998, Pyle 2008). Among definitive-cycle alcids, seasonal differences were found in five species, Parakeet *A. psittacula* and Crested *A. cristatella* auklets and all three puffins (ANOVAs: $F > 4.7$, $P < 0.05$). These species are known to shed plates or appendages that could affect bill width at the gape (Kozlova 1957, Gaston & Jones 1998).

Summary of molt strategies in alcids

The occurrence and timing of molts in North American alcids, based on specimen examination (see Table 1 for sample sizes), is represented diagrammatically in Fig. 2. Although only 4% of specimens examined were undergoing molt at time of collection (ranging from 0% in six species to 17% of Whiskered Auklets), timing and extent of molts could also be inferred from the presence of recently replaced feathers, contrasting with older feathers of a previous generation. Use of H-P terminology allows comparison of presumably homologous molts
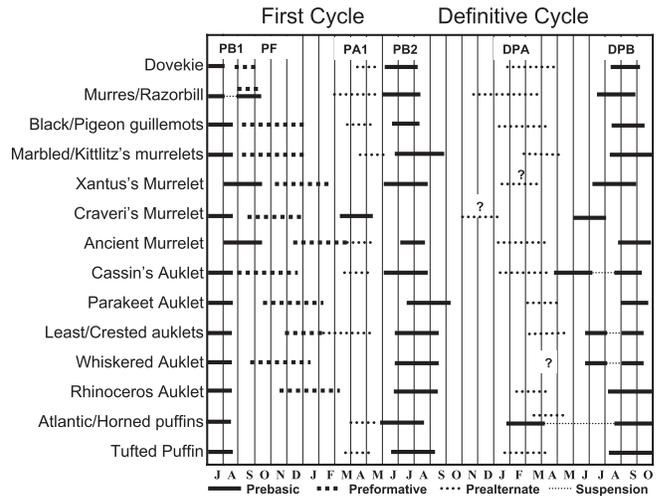

Fig. 2. Occurrence and timing of molts in alcids based on specimens examined in this study. Species are combined where molt strategies are similar. Molts are abbreviated as PB1 (first prebasic, traditionally known as "pre-juvenile"), PF (preformative, traditionally known as "first prebasic"), PA1 (first prealternate), PB2 (second prebasic), DPA (definitive prealternate), and DPB (definitive prebasic). Data are based on the timing of all (4%) specimens collected in molt and on the appearance of fresh feathers following periods of molt. Note that, within species, molts vary substantially by latitude, resource availability, and so on; the information here should therefore be interpreted as a species-wide generalization of molting strategies. All prebasic molts are complete in alcids, as indicated by solid bars; preformative and prealternate molts can be absent or partial, and potentially can merge (see text). Note that in puffins, third-cycle molts may differ in timing from definitive-cycle molts (Howell & Pyle 2005).

across taxa (Fig. 2), not always possible with conventional molting terminologies (see the subsections that follow).

First prebasic molt

The first prebasic molt (PB1) occurs at the nest site in June–August in most species, but has been delayed until after fledging in *Synthliboramphus* murrelets that fledge in downy plumage, before the first pennaceous feathers have erupted (Fig. 2). This and other molts are earlier in Craveri's Murrelet than in the other two *Synthliboramphus* species (Fig. 2), presumably because of its earlier breeding season. Timing in Xantus' Murrelets *S. hypoleucus* also appeared to average earlier in the more southern and earlier-breeding *S. h. hypoleucus* than in the more northern and later-breeding *S. h. scrippsi*. Otherwise, patterns and extent in these two subspecies appeared to be similar.

Molt terminology in murres and Razorbill during the fledging period can be interpreted in different ways. Careful tracing of molts in specimens revealed that natal down at hatching is replaced at the nest site by a coat of weak pennaceous feathers, which includes all body feathers, wing coverts and rectrices, but not primaries or secondaries. The juvenal primary coverts are stronger than most of the secondary coverts, including more tightly knit barbs and barbules, perhaps helping to simulate abbreviated primaries, so that fledglings can "parachute" from cliff-side nests when fledging. During the first months at sea, all juvenal body feathers, coverts and rectrices, with the exception of the primary coverts and some outer greater coverts in some birds (*cf.* Wilhelm *et al.* 2008), are replaced again concurrent with initial growth of primaries and secondaries. Based on presumed homologies with natal downs and first-cycle molts of other alcids, I consider the PB1 in murres and Razorbill to occur in two stages: body feathers, wing coverts and rectrices are replaced at the natal site; primaries and secondaries develop at sea (Fig. 2). A preformative molt (PF) then occurs, concomitant with first growth of the remiges during the first prebasic molt; it includes all body feathers and rectrices but not the remiges, primary coverts or the outer greater coverts in some birds. Thus, the primary coverts (and some secondary coverts in some birds) are the only feathers grown at the natal site that are retained through the first cycle, and contrasts between these feathers and coverts replaced during the partial preformative molt can be used to distinguish first-cycle from older birds (Wilhelm *et al.* 2008). For stable-isotope analyses, sampling from primary coverts in first-cycle murres and Razorbills will produce signals from the natal site (including diet provided by parents); sampling from primaries will produce diet and location signals corresponding to molting location at sea in July–September.

Inserted first-cycle molts

Nine alcid species appeared to exhibit two inserted molts within the first cycle, and 11 species appeared to have only one inserted molt (Fig. 2). In most of the species with two inserted molts, the first prealternate molt (PA1) occurred later in the season and was limited in extent (often to scattered head and body feathers) compared with the definitive prealternate molt (DPA) of the same species (Fig. 2). The PA1 appeared to be absent in some individuals of most of these species, presumably reflecting timing of fledging or poorer resource availability during the year the bird was collected (or both). Sampling from first-cycle birds of these species in spring and summer can yield up to three signals, those of the natal site (primaries for most species, but primary coverts in murres and Razorbill), fall-molting period

(most body feathers) and spring-molting period (scattered, fresher first-alternate feathers on the head and upperparts).

The single inserted first-cycle molt varied substantially in timing between the 11 species exhibiting this strategy (Fig. 2). In five species (Xantus' and Craveri's murrelets and Parakeet, Whiskered and Rhinoceros auklets), the single molt appeared to be comparable to a PF rather than to a PA1, generally occurring in fall rather than in the spring, and being more complete than are the DPAs of the same species. In the three puffins, the single molt appeared comparable to a PA1 rather than to a PF, occurring in spring and showing a similar extent (primarily head feathers) to the DPAs in the definitive cycle. In the remaining three species (Ancient Murrelet *S. antiquus* and Least *A. pusilla* and Crested auklets), the single molt spanned the winter and may have represented the merging of a PF and PA1 in ancestral species. It is not possible to determine from specimens whether or not a few feathers could have been replaced twice during inserted first-cycle molts in these three species (indicating, by definition, both a PF and a PA1), but these molts appeared more like a single protracted replacement of feathers. For these 11 species (displaying only a single first-cycle molt), natal signals (from primaries) and molting-site signals for various seasons (from replaced body feathers) can both be obtained during spring and summer (Fig. 2). The protracted first-cycle molts of some of these species may begin and end at different locations, allowing separate signals to be identified by sampling fresher and more worn feathers from the single inserted generation.

Second and definitive prebasic molts

In all species, the second prebasic molt (PB2) occurred earlier in the season than the DPB (Fig. 2), presumably reflecting lack of breeding and accompanying constraints in one-year-old alcids (*cf.* Bédard & Sealy 1984). Specimens of 12 species in second or definitive cycles showed primaries and secondaries that were uniform in wear [Fig. 3(a)], reflecting synchronous molt of wing feathers, known to occur in some species of alcids (*cf.* Stresemann & Stresemann 1966, Thompson *et al.* 1998, Thompson & Kitaysky 2004). Molt clines, suspension limits, or both (Pyle 2008), reflecting sequential or non-synchronous molts, were observed in the remaining eight species: Marbled *Brachyramphus marmoratus,* Kittlitz's *B. brevirostris,* Xantus', and Craveri's murrelets, and Cassin's *Ptychoramphus aleuticus,* Least, Crested, and Whiskered auklets. Some (but not all) specimens of definitive-cycle Marbled and Kittlitz's murrelets showed contrasts indicating that inner and outer primaries were replaced in blocks [Fig. 3(b)], with suspension most often between p5 and p6 or p6 and p7 (see also Carter & Stein 1995). For three species (Xantus' and Craveri's murrelets and Crested Auklet), most specimens had uniform primaries and secondaries indicating synchronous molts [Fig. 3(a)], but one to three specimens of each were found with replacement patterns in blocks [the two murrelet species—Fig. 3(b)] or with suspensions [Crested Auklet—Fig. 3(c)]. See also Harris & Yule (1977) for examples of Atlantic Puffins *Fratercula arctica* showing asynchronous wing molt not typical of that species.

Many Cassin's, Least, and Whiskered auklet specimens, along with one to two specimens of Crested Auklet (see earlier) displayed patterns indicating suspension of primary molt during the DPB of breeding individuals [Fig 3(c)—see also Payne 1965, Emslie *et al.*1990, Pitocchelli *et al.* 2003]. From one to five primaries appear to be replaced during incubation or early chick-feeding, followed

by suspension for the bulk of chick-feeding and resumption of sequential replacement of primaries after the breeding season. Other definitive-cycle individuals of these species showed uniform sequential replacement indicating that no suspension had occurred. These birds may have included second-cycle individuals, non-breeding (or failed-breeding) definitive-cycle individuals or perhaps some successfully breeding birds that failed to initiate molt during incubation. When a suspension limit among the primaries is detected on breeding birds the following year [Fig. 3(c)], it likely represents a breeding bird that can be aged in its third cycle or older, depending on age of first breeding in the species. Isotopic signals reflecting the previous breeding season can be obtained by sampling from the inner, more worn, primaries.

Molts in puffins showed unusual intra-generic variation, with Tufted Puffin *F. cirrhata* exhibiting a DPB resembling those of other large alcid species, and Atlantic and Horned *F. corniculata* puffins showing an interesting split DPB, primaries and secondaries being replaced in the early spring (concurrent with a DPA of head feathers), followed by suspension for breeding and resumption of the molt after breeding (Fig. 2—Harris & Yule 1977), a molt strategy also found in larger loons *Gavia* spp. Howell & Pyle (2005)
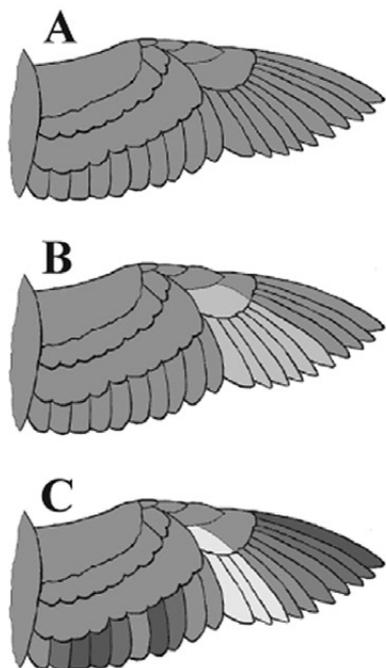

Fig. 3. Molt patterns apparent among the primaries and secondaries of alcids, reflecting (A) synchronous molt, (B) molt in blocks with suspension between p1–p6 and p7–p10, and (C) sequential molt following suspension of primary molt (after p1–p3 have been replaced) during breeding. Pattern A is found in most definitive-cycle individuals of 14 alcid species; pattern B is found in most definitive-cycle *Brachyramphus* murrelets and occasionally in Xantus's *Synthliboramphus hypoleucus* and Craveri's *S. craveri* murrelets; and pattern C is found in many definitive-cycle Cassin's *Ptychoramphus aleuticus,* Least *Aethia pusilla,* and Whiskered *A. pygmaea* auklets and occasionally in Crested Auklets *Aethia cristatella.* Some definitive-cycle Cassin's, Least, and Whiskered auklets, perhaps non-breeding individuals, show sequential patterns from p1 to p10, without suspension limits (A). It is unknown as yet how molt progresses in double-brooded individuals of Cassin's Auklets (*cf.* Ainley & Boekelheide 1990).

traced these molts in puffins and loons from the first through the definitive cycles and justified the terminology presented here.

Definitive prealternate molts

Fresher feathers in definitive-cycle individuals, indicating the occurrence of DPAs, were detected in at least a few spring and summer specimens of all but one species, Whiskered Auklet (Fig. 2). In 13 alcid species, aspect in alternate plumage varied from that of basic plumage, resulting in well-documented display coloration (breeding-plumage aspect), presumably an adaptation for sexual selection. Six of the remaining seven species (Xantus' and Craveri's murrelets and Parakeet, Crested, Whiskered, and Rhinoceros *Cerorhinca monocerata* auklets) did not have display plumages differing markedly between seasons (see later text concerning ornamental plumes) and appeared to have very limited DPAs, confined to, at most, a few feathers of the head, upperparts, breast and flanks. The positions of replaced breast and flank feathers coincided with the water line while floating. These feathers may have been replaced to help increase flotation, given that molt of such feathers was also found in waterfowl (Pyle 2005). For the two murrelets and the Whiskered Auklet, it was difficult to confirm whether a DPA occurs, as indicated by the question marks in Fig. 2. Cassin's Auklet had a surprisingly extensive DPA, given the lack of an ornate alternate plumage aspect, including most to all head and back feathers and up to half the secondary coverts. For species exhibiting a DPA, an additional spring-season signal, reflecting location during the prealternate molt, can be obtained by sampling display-colored or fresher body feathers in the spring and summer.

Ornamental occipital or facial plumes occur in seven species, Ancient Murrelet; Parakeet, Least, Whiskered, Crested and Rhinoceros auklets; and Tufted Puffin. These plumes have traditionally been considered part of alternate or "breeding" plumages, but specimen evidence suggests that, with the possible exception of the puffin, they are replaced only once per year, toward the end of PB2s and DPBs, and should be considered basic feathers. They appear to be specialized feathers, perhaps filoplumes, developing slowly over winter rather than replacing basic feathers and developing quickly in the spring (see Pyle & Howell 2004 for similar molts of ornamental plumes in herons and egrets, Ardeidae). Partial ornamental plumes can also be developed in some (but not all) individuals during the PF of these species. In Tufted Puffin, short brownish feathers occur in the supercilial area in fall, after ornamental tufts are shed. It is possible that these are basic feathers and that the tufts are alternate feathers. Alternatively, the tufts may arise from specialized follicles activated only once per year (as in the murrelets and auklets discussed earlier) and would thus be basic feathers.

DISCUSSION

Age determination in alcids by gape-width measures

Results of the present study indicate that gape width at the premaxillary process (Fig. 1) becomes significantly wider with age in all 20 North American alcid species. This measure is easy to obtain, and I suggest that the results in Table 2 can be used preliminarily and in combination with other criteria to help diagnose age in first-cycle and older alcids. However, it must be cautioned that gape-width results were obtained from specimens that were potentially subject to varying preparation methods or damage during collection, and therefore need confirmation; a small proportion of measurements

fell far outside of expected ranges for a species–age group. I encourage further sampling of freshly killed and live (preferably known-age) alcids to confirm and refine the results presented here. I also encourage examination of the remaining three species of extant alcids, Spectacled Guillemot *Cepphus carbo,* Long-billed Murrelet *B. perdix* and Japanese Murrelet *S. wumizusume,* for which too few specimens were available in the museums visited to perform adequate analyses. Molt and age criteria for these species appeared to parallel those for Pigeon Guillemot *C. grille,* Marbled Murrelet and Ancient Murrelet respectively (Pyle 2008, specimen examination), and it can be predicted that gape-width measurements will be similar as well.

The premaxillary process appears to continue widening until at least two full years of age, and it is possible that additional gape-width criteria could be established to distinguish second-cycle individuals in species that lack distinctive second-cycle plumage aspects. Confidence intervals established from live birds by sex and season would further assist with age and sex determinations of certain species (see "Results").

Molt strategies in alcids

Several results presented here regarding molt strategies are novel or contrast with published information. Part of the problem with some previous summaries is the use of terminologies that do not attempt to trace homologous molts and plumages, which can lead to erroneous assumptions about molts. For example, in species with a single protracted first-cycle molt, traditional terminology often results in the definition of two molts, preformative ("post-juvenile") and first prealternate ("first prebreeding," even though the individuals do not breed), based on seasonal timing of feather replacement, when in fact there is just one molt. Furthermore, the interesting definitive molts of Atlantic and Horned puffins, like those of certain loons, have been considered complete "prebreeding molts" followed by partial "postbreeding molts" or have been assumed to involve delayed primary molts following breeding (Palmer 1962, Harris & Yule 1977, Cramp & Simmons 1985, Gaston & Jones 1998). However, tracing these molts from the first cycle indicates that the prebasic molt begins in winter or early spring, overlapping a partial prealternate molt, and then concludes in fall with body feathers (Howell & Pyle 2005).

Ornamental plumes in murrelets and auklets have long been considered part of "breeding" or alternate plumage, developed during a "prebreeding" or prealternate molt, because they are most apparent in spring, when adults return to colonies (Bédard & Sealy 1984, Cramp & Simmons 1985, Gaston & Jones 1998); however, careful tracing of molts reveals that they are more likely basic ("postbreeding") feathers. Although Bédard & Sealy (1984) used H-P terminology, they miscategorized first prealternate molts as occurring in the second cycle (presumably based on the presence of formative ornamental plumes in some first-cycle birds), which in part apparently led them to misclassify one-year-old first-cycle auklets as two-year-old birds (*cf.* Pyle 2008).

The use of H-P terminology not only clarifies the nomenclature of molts but puts them in a framework to attempt tracing their evolution. Molt strategies vary substantially in alcids, which can display the Complex Alternate, Simple Alternate and Complex Basic strategies described by Howell *et al.* (2003). Few other families display such variation. Variations in molt patterns within alcid genera such as *Synthliboramphus* and *Fratercula* indicate

that molts may be subject to fairly rapid evolution based on environmental constraints. A comparison of molt strategies with proposed phylogenies of Charadriiformes (Baker *et al.* 2007) and alcids (Strauch 1985; Moum *et al.* 1994, 2002; Friesen *et al.* 1996), latitudes of occurrence, migratory and foraging strategies, and other species-specific life-history traits, in an attempt to understand the evolution of and environmental constraints on molts, would make an interesting subject for further study. Preliminarily, I suggest that ancestral alcids exhibited a Complex Alternate Strategy (as do many other Charadriiformes), and that inserted molts have been lost or merged in certain species because of environmental conditions and constraints.

Sampling of feathers for stable isotope analyses

Stable isotopes and other signals obtained from feathers are currently being used to study various aspects of avian natural history (Hobson 1999, Pyle *et al.* 2008), including those of alcids (e.g. Becker & Beissinger 2006, Moody & Hobson 2007), but knowledge of molt patterns is necessary to determine the phase of the annual cycle being sampled. Results of the present study can be used as a guide to help obtain up to three isotopic signals from a single individual, not only increasing sample sizes from fewer collected or captured birds, but possibly also establishing individual connectivity between breeding, molting and non-breeding grounds. Although I believe the strategies proposed here may advance the current understanding concerning timing and location of molts, specimen data are not always adequate to detect or trace molts, and confirmation of these results thus may be needed from live known-age birds. I encourage those undertaking stable-isotope analyses on alcids to attempt to identify feather generations, to sample feathers from several tracts and to use stable isotopes not only to investigate foraging patterns and diet, but also to help confirm the general molting patterns presented in the present analysis (*cf.* Pérez & Hobson 2006, Fox *et al.* 2007).

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