Molt, Age Determination, and Identification of Puffins

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The Institute for Bird Populations P.O. Box 1436 Point Reyes Station CA 94956 ppyle@birdpop.org ong-lived seabirds, including puffins, typically defer breeding until three or more years of age, and their first year or two of life are spent at sea, away from breeding colonies. In such species the timing and extent of molts are poorly known. Few specimens exist, field study of live birds is often hindered by difficult observation conditions, and a bird's precise age is usually unknown and instead must be inferred. Individual variation in plumage aspect (i.e., color and pattern), bare-part development, and the timing and extent of molt further cloud the picture, even within age-groups. And all of this complexity is superimposed upon inter-annual variation in food resource availability, which may further influence molt timing and, in years of breeding failure, may lead to the absence of an entire age-class (Ainley and Boekelheide 1990).

The impetus for this investigation was frequent debate on the identification and age of immature puffins observed on pelagic trips off California. Species identification is greatly facilitated, however, once a simple factor is appreciated: First-year Tufted Puffins can have white underparts (Fig. 1a). This feature is treated variably in field guides. For example, Sibley (2000) indicates that juvenile Tufted Puffins are all-dark below, whereas NGS (2002) states that juveniles can have "white or dark underparts" and illustrates both types.

While examining specimens for identification criteria, we began to investigate the prerequisite and (at least to us) more interesting topics of molt sequence and age determination. Here we present a preliminary summary, based largely on specimen examination, of molt and aging in Tufted and Horned Puffins. Species determination happens to be useful for understanding these topics, so we start with a brief synopsis of field identification criteria.



Identification of adult Horned and Tufted Puffins in breeding plumage is straightforward. But what of individuals in other plumages? In order to make sense of these more-difficult plumages, it is essential to have a basic grasp of molt and aging. The approach in this article is to examine in some detail various characters that are evident from a study of museum specimens—with the hope that the lessons learned can be put to good use at sea. Adult **Tufted Puffin** in transition to non-breeding plumage. Santa Cruz County, California; September 2004.

Mike Danzenbaker.

IDENTIFICATION

Juveniles of both Tufted and Horned Puffins have relatively narrow, dark-orangish bills that lack the distinctive shape and coloration which readily distinguish adults. Both species also share generally dusky heads and upperparts, and white to whitish bellies, but they still show certain adult-like plumage criteria that enable species identification throughout the first year (Fig. 1). For those with open minds and lofty goals, separation of first-year Horned Puffin from Atlantic Puffin can usually be accomplished by examination of the throat and face patterns (Fig. 2). A Horned Puffin reached Mackenzie, North West Territories, and a Tufted Puffin made it to Maine (AOU 1998); populations of two ostensibly Atlantic alcids, Dovekie and Black Guillemot, have crossed the Arctic to inhabit the Bering Sea; and Long-billed and Ancient Murrelets have made long-distance flights all the way to the Atlantic Seaboard. Hence, pelagic observers in both oceans should be familiar with criteria to distinguish non-breeding plumages of Horned and Atlantic puffins, just in case...

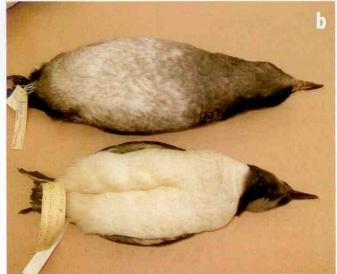
MOLTS

The molts of both Tufted and Horned Puffins are poorly known (summarized by Gaston and Jones 1998; Piatt and Kitaysky 2002a, 2002b; Thompson and Kitaysky 2004). Adults of both species acquire their breeding plumage in spring and their non-breeding plumage in fall, but little or conflicting information exists on the timing of flight-feather molts (here also simply termed "wing molts"), which, in puffins, are synchronous (i.e., all remiges are dropped almost simultaneously, rendering birds flightless). Essentially nothing has been published concerning pre-definitive molts (i.e., the molts of immatures before they attain the definitive plumage aspect).

Piatt and Kitaysky (2002a, 2002b) inferred that definitive molts are similar between the species, but our specimen data indicate distinct differences (Fig. 3). Whereas adult Tufted Puffins typically undergo wing molt during late fall and early winter, adult Horned Puffins molt their remiges (and upperwing coverts and tail) in spring, a strategy similar to that of the Atlantic Puffin (Salomonsen 1944, Harris and Yule 1977, Cramp and Simmons 1985). These divergent molt strategies show an interesting parallel to those of loons: Red-throated Loon exhibits a sequence similar to that of Tufted Puffin, whereas Pacific and Common Loons have a sequence similar to that of Horned Puffin (Palmer 1962, Woolfenden 1967).

Interpreting the molt sequences of puffins and loons







presents an interesting challenge to the application of Humphrey and Parkes's (1959) terminology for molts and plumages. If one simply considers the adult strategies, which is usually how presumed homologous molts have been determined, then it seems reasonable to conclude that adult Horned Puffins *delay* their wing molt until spring, as has been proposed for Pacific and Common Loons (Palmer 1962, Woolfenden 1967). However, if one reviews the sequence of wing molts in loons and puffins starting with juveniles, then a different interpretation is suggested (Fig. 3).

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In their second calendar-year, all species of puffins and loons undergo a wing molt from spring through late summer, the timing varying somewhat among (and within) species. Species-specific differences become evident in the third and subsequent calendar years (Fig. 3). Note, though, that if adult wing molts really are *delayed* in Horned Puffin and in larger loons, then their second-calendar-year wing molt (labeled PB2 in Fig. 3) would be a novel or inserted molt relative to the strategy of Tufted Puffin and Redthroated Loon (see Fig. 3), and thus should be considered a prealternate or presupplemental molt according to Humphrey-Parkes nomenclature.

It is of course possible that an additional wing molt has evolved in some species but not in others; and it is also possible that molts have shifted from an ancestral pattern, such that a complete prebasic molt now occurs in spring. This latter interpretation would mean that the bright "breeding plumage" is the basic plumage, as has been argued recently for ducks (Pyle 2005), and which emphasizes the important distinction between homologies of molt and homologies of color (Howell et al. 2004). We suggest that it is easier for hormones which control color to shift temporally than for entire prebasic molts to shift (but short-duration synchronous wing molts may be more flexible). It is therefore more parsimonious to view second-calendar-year wing molts as being homologous in all puffins and loons (Fig. 3). Second-calendar-year wing molts are shared by many species, suggesting that they are part of an ancestral pat-

Consequently, relative to the molts of Tufted Puffin and Red-throated Loon, the third and subsequent calendar-year

Fig. 1. Three comparisons of first-year Tufted Puffin (upper) and Horned Puffin (lower). The underparts of Tufted Puffins vary from white with a pale gray throat (a) to grayish with a dusky throat (b); but note the lack of distinct contrast between the dark throat and white breast as with Horned Puffin. First-year Horned Puffins also show the well-defined grayish auricular region found in basic-plumaged adults, whereas in Tufted Puffins the face is typically dark with the hint of a pale supercilium, a precursor to the breeding tufts developed later in life (c). These criteria are similar throughout the first year of life. Specimens in (a): collected in February off Japan. Tufted Puffin specimens in (b) and (c): collected in August off Oregon. Horned Puffin in (b) and (c): collected in September in Alaska. © Peter Pyle.

wing molts of Horned Puffin and larger loons are simply occurring *before* the breeding season, not being delayed. Thus, their prebasic molt is split, with the wing feathers renewed in spring (overlapping with the prealternate molt of head feathers), and the head and body feathers in fall to early winter (Fig. 3). Another Arctic-breeding species, the Ivory Gull, also molts most of its primaries prior to breeding, starting in March or April (Howell 2001); if it had synchronous wing molt like puffins and loons, rather than the more-common sequential molt (one primary at a time), then its wing molt would also be completed in spring. Thus, for certain Arctic-breeding, shorter-distance migrants, more resources for wing molt appear to be available before the breeding season than in the short period between the end of breeding and the onset of winter.

It thus appears that both puffins and loons exhibit the Simple Alternate Molt Strategy (Howell et al. 2003). The provisional molt schedules for puffins shown in Fig. 3 will undoubtedly require modification as more data from wild birds are acquired; even the extent of prealternate molts needs to be clarified. Note that definitive prebasic molts probably occur earlier in the season in failed breeders and non-breeders. The ornamental bill plates are shed mainly in late August – October and regrown mainly in March – early May.

PLUMAGE SEQUENCES AND AGE DETERMINATION

The results of our specimen examination suggest that Tufted and Horned Puffins can be aged through their second (Horned) or third (Tufted) calendar-year by plumage aspect. The ages of adults may be further inferred by size and shape of bill plates and the number of bill-plate grooves, as documented in known-age Atlantic Puffins (Harris 1981) and inferred for Tufted Puffins (Tanaka and Ogi 1986; Fig. 6).

Tufted Puffin apparently requires three years to obtain brownish-black underparts (often with some whitish mottling), a pattern it then retains for life (Fig. 4). The elongated head plumes and ornamental bill plates of breeding adults appear not to develop fully until the fourth or fifth calendar-year (Fig. 5; Tanaga and Ogi 1986). By this age, however, individual variation in maturation rates may cause overlap between advanced individuals of one agegroup and retarded individuals of the next-oldest agegroup, so caution is warranted.

Horned Puffin shows less variation in plumage aspect by age, with the white underparts and breeding head pattern not varying with maturity as in Tufted Puffin. First-spring birds have a gray face and dusky lores, similar to juvenal and definitive basic plumages, after which the definitive





Fig. 2. Two comparisons of first-year Horned (top & left) and Atlantic (bottom & right) Puffins. Adult Horned Puffins have a blackish chin and throat, whereas adult Atlantic Puffins have the grayish malar region and chin separated from the white breast by a distinct dark band. These features are also shown by first-year birds, although somewhat less distinctly. The combination of blacker upperparts and breast with a more-distinct breast band and paler throat should allow separation of most first-year Atlantic from first-year Horned Puffins at sea. Differences in bill shape (see Sibley 2000) begin to be expressed in second-year and older birds. Horned Puffin: collected in September in Alaska. Atlantic Puffin: collected in August in Iceland. © Peter Pyle.

plumage aspect is attained (Fig. 7). Thus, from second-basic plumage onward, age must be inferred by bill-groove criteria. Variation in length of the eponymous horn (a keratinous protuberance) might also repay investigation as a possible aid to aging.

We conclude by cautioning readers that our summary is based on specimens of unknown-age birds; therefore, much

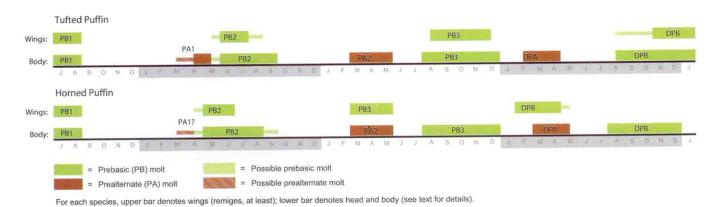


Fig. 3. Provisional molt timings in Tufted and Horned Puffins, showing sequences and presumed homology of wing molts. Note how strategies diverge between the species in the third and subsequent calendar years, with wing molts becoming progressively later in Tufted Puffin, but earlier in Horned Puffin.

Tufted Puffins fledge primarily in August—September and apparently retain juvenal plumage (i.e., first basic plumage, following Howell et al. 2003) through the winter. The complete second prebasic (PB2, etc.) molt in wild birds occurs mainly during June—September of the second calendar-year, preceded by a limited first prealternate (PA1, etc.) molt in May. In the third calendar-year there is a partial PA2 molt in March—May and a complete PB3 molt during August—December. Subsequently, the definitive molt cycle is adopted, with DPA molts in February—April and DPB molts mainly in September—January.

Horned Puffins fledge mainly in September and also appear to retain juvenal plumage through the winter. The complete PB2 molt occurs mainly during May—August of the second calendar-year (possibly preceded by a PA1 molt in spring). The partial PA2 molt of head feathers overlaps with PB3 wing-molt in March—May of the third calendar-year, and the PB3 body-molt completes in August—December. Subsequently, the definitive molt cycle is adopted: DPB wing-molts in February—April overlap with DPA body-molts in March—May, with DPB molt of body feathers completing in August—December.

Piatt and Kitaysky (2002b) suggested two wing molts for second-calendar-year Tufted Puffins, reflecting two confounding issues that should be clarified. First, they equated first-winter plumage with a complete first-prebasic molt at one year of age, contra Dement'ev and Gladkov (1951). Second, they assumed that a wing-molt schedule exhibited by captive second-calendar-year birds in February to April (detailed by Thompson and Kitaysky 2004) equated to that of wild birds, despite other authors' having reported this molt as occurring in June and later (Kuroda 1955, Hamilton 1958, Stresemann and Stresemann 1966), which agrees with our specimen examination. Inferences based on the timing and extent of molt in captive birds should be treated with caution: For example, some captive Atlantic Puffins molt their flight feathers twice, and others once, in their second and third calendar-years (Swennen 1977). Figure by © Kei Sochi.



Fig. 4. Variation in underpart plumage aspect by age in Tufted Puffin. Juveniles (left; also see Fig. 1) show variable amounts of whitish, birds in second-basic plumage have grayish bellies blending to darker throats (center), and birds in definitive plumage have uniformly blackish-brown underparts (right). These patterns in underpart plumage are shown yearround, as only head feathers are replaced twice per annual cycle. Juvenile, left: collected in February in Japan. Second-basic, center: collected in August in Alaska. Individual just completing definitive prebasic molt, right: collected in January in Oregon. © Peter Pyle.

has had to be inferred. Nevertheless, we are confident that our conclusions provide a greatly improved launching pad for further investigations, which will preferably involve known-age birds. Active pelagic birders can also help by photographing birds at sea, recording data on birds in wing molt, noting eye-color and other bare-part color changes on live birds, and depositing in museum collections any dead birds found.

Acknowledgments

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Literature Cited

Ainley, D.G., and R.J. Boekelheide, eds. 1990. Seabirds of the Farallon Islands. Stanford University Press, Stanford.

American Ornithologists' Union [AOU]. 1998. *Check-list of North American Birds*, seventh edition. American Ornithologists' Union, Lawrence.

Cramp, S., and K.E.L. Simmons, eds. 1985. The Birds of the Western Palearctic, vol. IV. Oxford University Press, Oxford.

Dement'ev, G.P., and N.A. Gladkov, eds. 1951. *Birds of the Soviet Union*, vol. 2. Soviet Academy of Sciences, Moscow.

Gaston, A.J., and I.L. Jones. 1998. The Auks. Oxford University Press, New York.Hamilton, W.J. 1958. Pelagic birds observed on a North Pacific crossing. Condor 60:159–164.

Harris, M.P. 1981. Age determination and first breeding of British puffins. British Birds 74:246–256.

Harris, M.P., and R.F. Yule. 1977. The moult of the Puffin Fratercula arctica. Ibis 119:535–541.

Howell, S.N.G. 2001. Molt of the Ivory Gull. Waterbirds 24:438-442.

Howell, S.N.G., C. Corben, P. Pyle, and D.I. Rogers. 2003. The first basic problem: A review of molt and plumage homologies. *Condor* 105:635–653.

Howell, S.N.G., C. Corben, P. Pyle, and D.I. Rogers. 2004. The first basic problem revisited: Reply to commentaries on Howell et al. (2003). *Condor* 106:206–210.

Humphrey, P.S., and K.C. Parkes. 1959. An approach to the study of molts and plumages. *Auk* 76:1–31.

Kuroda, N. 1955. Observations on pelagic birds of the northwest Pacific. Condor 57:290–300.

National Geographic Society [NGS]. 2002. Field Guide to the Birds of North America, fourth edition. National Geographic Society, Washington.

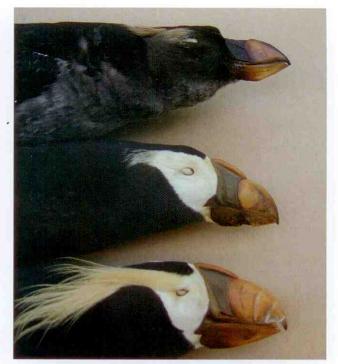


Fig. 5. Variation in alternate plumage aspects of pre-definitive and definitive Tufted Puffins. Two-year-old birds (in second-alternate plumage; top) typically acquire a rudimentary crest, may or may not develop paling of the auricular and loral regions, and have a relatively narrow and smooth bill. The center bird is probably 3 years old (in third-alternate plumage); it has developed a white face and deeper bill (with 1 or 2 grooves; see Fig. 6), but it lacks an extensive crest (although some crest-plumes may already have been shed during an early start of the fourth prebasic molt). The individual at the bottom shows full development of the breeding plumes and a fully developed bill with 4 grooves (see Fig. 6). Specimens collected along the Pacific North American coast in April (top), August (center), and June (bottom). © Steve N. G. Howell.

Fig. 6. Variation in bill development in definitive-alternate (a) and definitivebasic (b) Tufted Puffins. The alternateplumaged birds (all from June) show 2 (top), 3 (center), and 4 (bottom) grooves beyond the ridge bordering the keratinous cere. The cere and bill shield are shed in fall, such that basic-plumage birds (mainly during September-February) have smaller bills. These show 2 (top), 3 (center), and 2 (bottom) grooves beyond the ridge (which also resembles a groove at this time). Based on bill-groove development (Tanaga and Ogi 1986), the alternate-plumaged bird at top is 3 years old, the basic-plumaged birds at top and bottom are at least 3 years old, and the other birds are at least 4 years old. Specimens collected along the North American Pacific coast in June (a) and November-January (b). © Steve N. G. Howell.







Fig. 7. Variation in plumage and bill size by age and season in Horned Puffins. From top to bottom, these are in juvenal, first-alternate, second-basic, presumed second-alternate, definitive-basic, and definitive-alternate plumage. Note that definitive plumage aspect is acquired after the second prebasic molt, but that subsequent aging can probably be accomplished by bill size and number of bill grooves. Horned Puffins develop fewer bill grooves than Tufted Puffins (see Fig. 6), such that individuals with 1 or 2 grooves are probably 2–3 years old and those with 2 or more grooves are probably at least 3–4 years old. Specimens collected

along the North American Pacific coast (primarily Alaska) in September, March, December, August, February, and August (from top to bottom). © Steve N. G. Howell.

Palmer, R.S. 1962. Handbook of North American Birds: Vol. 1. Loons through Flamingos. Yale University Press, New Haven.

Piatt, J.F., and A.S. Kitaysky. 2002a. Horned Puffin (*Fratercula corniculata*), in: A. Poole and F. Gill, eds. *Birds of North America*, no. 603. Birds of North America, Philadelphia.

Piatt, J.F., and A.S. Kitaysky. 2002b. Tufted Puffin (*Fratercula cirrhata*), in: A. Poole and F. Gill, eds. *Birds of North America*, no. 708. Birds of North America, Philadelphia.

Pyle, P. 2005. Molts and plumages of ducks (Anatinae). Waterbirds 28:207–218.

Salomonsen, F. 1944. The Atlantic Alcidae. *Göteborgs Kungliga Vetenskaps och Vitterhetssamhälles Handlingar* Följen 6, Ser. B 3:1–138.

Sibley, D.A. 2000. The Sibley Guide to Birds. Knopf, New York.

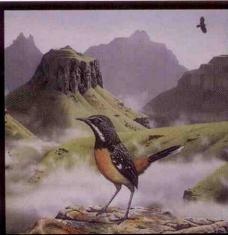
Stresemann, E., and V. Stresemann. 1966. Die Mauser der Vögel. *Journal für Ornithologie* 107:1–448.

Swennen, C. 1977. *Laboratory Research on Seabirds*. Netherlands Institute for Sea Research, Texel.

Tanaga, H., and H. Ogi. 1986. Evaluation of bill furrows as age indicator in the Tufted Puffin *Lunda cirrhata*. *Memoirs of the National Institute of Polar Research* 44:160–166.

Thompson, C.W., and A.S. Kitaysky. 2004. Polymorphic flight-feather molt sequence in Tufted Puffins (*Fratercula cirrhata*): A rare phenomenon in birds. *Auk* 121:35–45.

Woolfenden, G.E. 1967. Selection for delayed simultaneous wing molt in loons (Gaviidae). *Wilson Bulletin* 79:416–420.



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