FEATURED PHOTO

DARK-FACED COMMON MURRES OFF CENTRAL CALIFORNIA IN FALL AND WINTER

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ABSTRACT: While most basic-plumaged Common Murres (*Uria aalge*) show white facial plumage and tips to the secondaries, some individuals off central California from September through November have dark faces and secondaries. To investigate the plumage state and age of such birds, I examined specimens and photographs of Common Murres taken off central California and conclude that outgoing and incoming alternate feathers as well as early-replaced and late-replaced dark basic and formative feathers all may contribute to this variation. Hypermelanism may account for a small proportion of cases. The early onset of prebasic molt—before hormone signaling switches from dark feathers typical of the alternate plumage to white feathers typical of the basic plumage—may be responsible for most of the darkest-faced birds in basic plumage. This type of asynchrony of molt and the signal for change in plumage appears to occur more often in second-cycle birds, which initiate the prebasic molt earlier than do older adults, and it may also explain plumages in chicks and juveniles molting during May and June. Common Murres in basic plumage from colonies in central California appear to acquire dark facial feathers more often than birds from more northerly colonies, which could relate to earlier breeding and molt in central California.

The definitive prealternate molt of Common Murres (*Uria aalge*) breeding in central California can commence as early as November, rather than extending from January through April as in most other alcids and waterbirds (Ainley et al. 2002, Pyle 2008, 2009). The definitive prebasic molt in these murres occurs just after breeding, from July through September, at which time they lose the fully dark-headed alternate plumage and typically gain white basic feathering in the face, including the sides of the nape, posterior portion of the auriculars, subauricular area, chin, and throat. Because of the early start of the prealternate molt, full basic plumage may therefore be worn for as little as one to two months from September to November, as is the case in the more southern populations of the Common Murre breeding in the Atlantic (Harris and Wanless 1990). Populations of the Common and Thick-billed (*U. lomvia*) murres that breed farther north undergo prealternate molt later and can retain full basic plumage into March (Ainley et al. 2002, Gaston and Jones 1998, Pyle 2008). The earlier timing of the prealternate molt in central California populations may reflect the earlier breeding cycle of these birds, as adults begin occupying colonies as early as late October (Ainley and Boekelheide 1990), much earlier than at northern colonies (Gaston and Jones 1998, Ainley et al. 2002).

Although most basic-plumaged Common Murres show white faces, individuals with partially or completely dark faces occur off central California from September through November. The upper image on this issue's outside back cover shows a typical white-faced Common Murre in basic plumage; the lower shows a partially dark-faced individual. Both were photographed

on 7 October 2012 near Cordell Bank off Bodega Bay, California. A dark face has been used as a field mark to distinguish the Thick-billed from the Common Murre in basic plumage (Roberson 1980, Stallcup 1990, Gaston and Jones 1998), so the occurrence of dark-faced basic-plumaged Common Murres off central California needs to be further understood, and other field marks are needed to distinguish the two murre species (CBRC 2007).

Dark-faced adult Common Murres in fall could result from any or all of three molt/plumage scenarios: (1) a late or incomplete definitive prebasic molt, resulting in worn retained dark alternate feathers in the face; (2) an early definitive prealternate molt, resulting in fresh or incoming dark alternate feathers in the face; and/or (3) definitive basic feathers in the face that are dark or partially dark. Similarly, first-cycle murres might show dark or partially dark rather than white formative feathers in the face. To investigate these possibilities, I examined 221 specimens of post-juvenile Common Murres collected in California and housed at the California Academy of Sciences (CAS; 168 specimens) and Museum of Vertebrate Zoology (MVZ; 53 specimens). I also observed and photographed Common Murres during nine pelagic field trips off central California between Fort Bragg and Half Moon Bay from August through November in 2011 and 2012.

METHODS

I used the presence of emerging or pin feathers to indicate active molt in the faces of murre specimens. For each specimen in full basic or formative plumage (in which evidence of molt was lacking), and for murres observed in the field, I scored the face as (1) entirely or almost entirely white, (2) primarily white with sparse dark flecking, (3) primarily white with moderate dark flecking, or (4) primarily dark with some white feathering (Figure 1). The amount of white on the tips of juvenal and basic secondaries also varied; on specimens I scored this trait as (1) wide, (2) moderate, (3) thin, or (4) absent (Figure 2). I categorized specimens as first-cycle or adult on the basis of differences in color of the primary coverts, bill size and color, and bill width at the gape (Pyle 2008, 2009; Figure 1); in the field, I aged murres by bill size and color. Second-cycle murres could not be aged by plumage after completion of the second prebasic molt. However, I inferred that specimens with bill widths at the gape in the bottom quarter of the range for birds after their first cycle (19.6–20.7 mm of the full range 19.6–23.8 mm; Pyle 2009) were in their second cycle. This approach is consistent with results of bill-width data from other alcids that can be confirmed as second-cycle by plumage or other features. Sex was assumed from information on specimen labels.

RESULTS

Among adult specimens of the Common Murre from central California, 36 were collected while undergoing definitive prebasic molt. These birds had worn, dark alternate head feathers mixed with incoming white feathers. They ranged in date from 8 July (CAS 10020 with a few incoming white basic feathers) to 2 October (CAS 15796 with a few remaining alternate feathers). In addition, a one-year-old individual (MVZ 145340) collected from

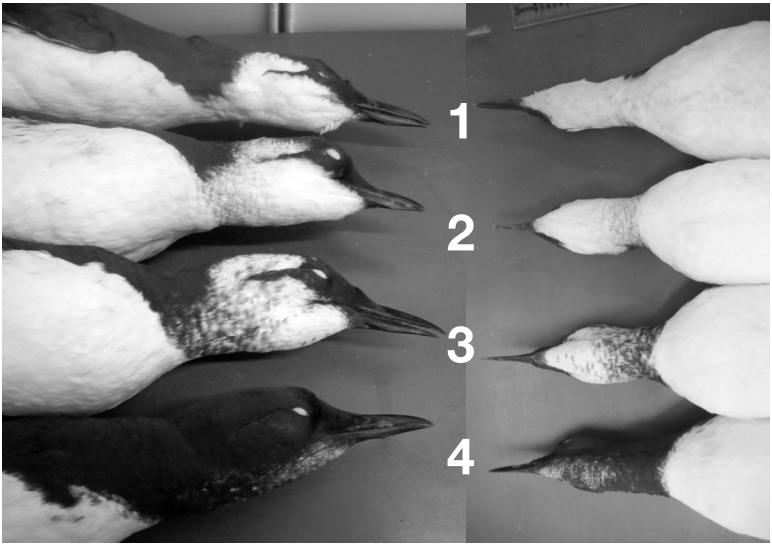

Figure 1. Four categories of variation in the facial plumage of the Common Murre in central California: (1) entirely or almost entirely white (CAS 43160, 12 February 1901), (2) primarily white but with sparse dark flecking (CAS 15784, 4 October 1909), (3) primarily white but with moderate dark flecking (CAS 16082, 13 December 1909), and (4) primarily dark but with some white (CAS 16078, 22 November 1909). Left, side view, and right, ventral view of the same specimens. All specimens were collected in Monterey Bay. CAS 15784 is in formative plumage; the other three specimens are in basic plumage.

Carmel Bay on 16 May was molting in white facial feathers with black tips (Figure 3A and B), as was another one-year-old, also collected 16 May, from Admiralty Island, Alaska (MVZ 69). Concurrent replacement of back, rump, and underpart feathers, as well those of the head, indicated that they were undergoing the second prebasic rather than the first prealternate body molt.

Thirty specimens of adults had been collected while undergoing definitive prealternate molt of the head, with the incoming feathers dark. The range of dates for these was 8 November (CAS 16077 with a few incoming alternate feathers) to 17 January (MVZ 75130 with a few basic feathers remaining and being replaced). The range of dates for 64 adults collected in fully dark (alternate) head plumage was 9 December (CAS 16070) to 27 August (CAS 15478 and 15482). I also observed a Common Murre with fully dark alternate head plumage off Half Moon Bay on the earlier date of 22 Nov 2011, the only such individual of more than 100 murres I scrutinized on this date. Two murres collected in June and July (CAS 68 and 75127) showed fully dark heads except for white tipping to some of the alternate face feathers (Figure 3C and D).

Sixty-one specimens of basic-plumaged adults, without outgoing or

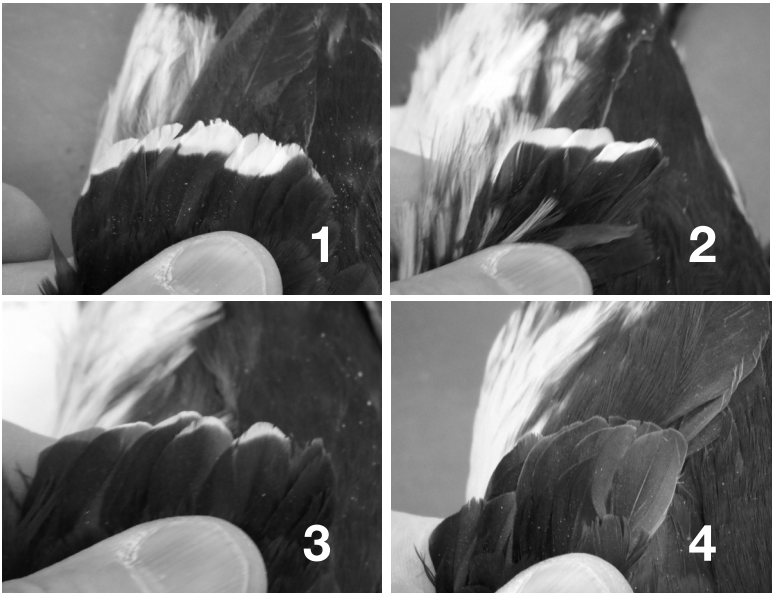

Figure 2. Four categories of variation in the width of white tips on the secondaries of the Common Murre in central California: (1) wide (CAS 15784, 4 October 1909), (2) moderate (CAS 16072, 26 November 1909), (3) thin (CAS 15793, 15 October 1909), and (4) absent (CAS 16078, 22 November 1909). All specimens were collected in Monterey Bay.

incoming alternate feathers, had been collected in California between 16 September (CAS 15786) and 15 March (CAS 10024, after second cycle). Other than the latter specimen and those collected 12 February (CAS 43160, after second cycle; Figure 1) and 24 February (MVZ 17756, second cycle), all basic-plumaged murres were collected between mid-September and early January. Twenty-nine first-cycle birds in formative plumage (lacking juvenal or, apparently, first alternate body feathers) were collected between 18 August (CAS 48176) and 9 April (MVZ 145352).

Birds in complete basic and formative plumage showed varying amounts of dark in the face (Figures 1 and 4; images on inside and outside back cover). In all cases, the dark coloration resulted from white-based basic feathers with dark tips of varying width (Figure 1). By contrast, alternate feathers were entirely dark. Murres with facial-plumage scores of 2 or 3 typically showed white on the sides of the nape and in the auricular and malar regions but dark-tipped throat feathers. By contrast, those with a plumage score of 4 typically displayed dark on the sides of the nape and in the auricular and malar regions but whiter throats (Figures 1 and 4).

The mean facial score was greater in basic-plumaged (2.26, $n = 61$) than in formative-plumaged (1.76, $n = 29$) Common Murre specimens (Figure 5; ANOVA, $P = 0.006$). Facial-plumage scores of specimens were similar to

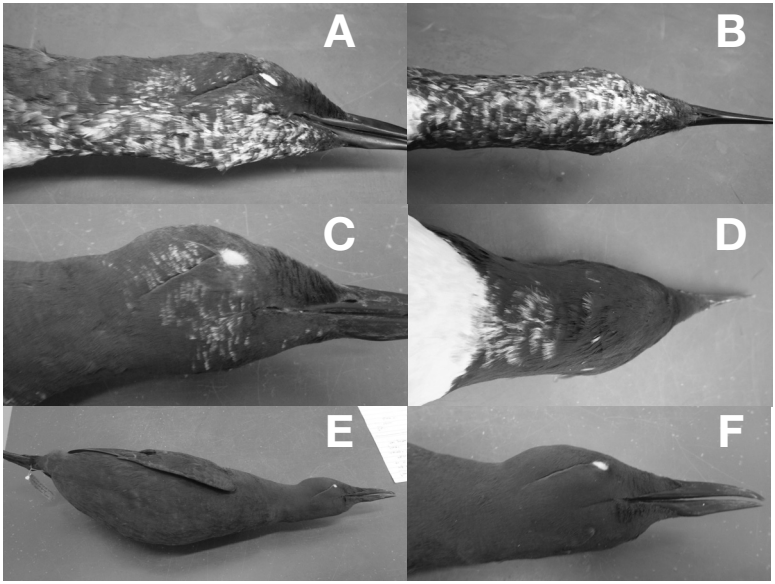

Figure 3. Variation in the molts and plumages of the Common Murre in central California. A (side view) and B (ventral view): MVZ 145340 (Carmel Bay, 16 May 1925), collected during presumably the second prebasic molt, with incoming feathers dark-tipped. C (side view: CAS 75127 (25 July 1903, San Francisco Bay) and D (ventral view): CAS 43166 (Monterey Bay, 19 June 1897), showing white tipping to alternate face feathers. E and F: CAS 18072 (Southeast Farallon Island, 30 May 1911), showing completely dark plumage.

those for both basic-plumaged (n = 209) and formative-plumaged (n = 100) murres scored on four pelagic trips off Half Moon Bay and Bodega Bay between 30 September and 6 November, when few or no alternate feathers should be expected on the basis of specimen data (Figure 5; P = 0.30 and 0.78, respectively). By contrast, both basic-plumaged (n = 55) and formative-plumaged (n = 31) murres scored off Fort Bragg in northern California on 6 November 2011 showed significantly less dark in the face than did specimens and live birds scored off central California (Figure 5; $P <$ 0.007 for each of four comparisons); none of the murres off Fort Bragg had facial scores of 3 or 4. Among specimens in basic plumage, faces of females averaged slightly darker than those of males (mean score: female 2.35, n = 26; male 2.15, n = 34), but this difference was not significant (P = 0.432).

The amount of white on the tips of the secondaries averaged less in basic-plumaged (mean score 1.66, n = 61) than in formative-plumaged (mean score 1.41, n = 29) specimens, but this difference was not significant (ANOVA; P = 0.084). As with facial score, the sexes had a similar amount of white in the secondaries (P = 0.278). Among basic-plumaged birds, the mean score for white in the secondaries was 1.07 for facial score 1 (n = 15),

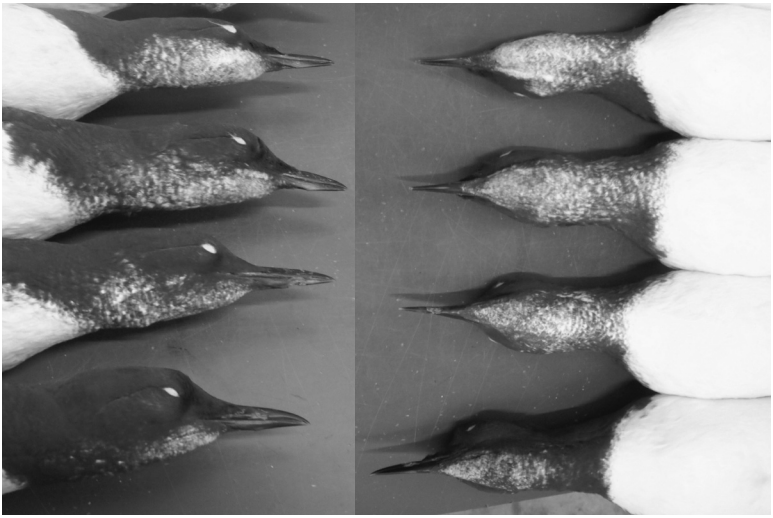

Figure 4. Dark-faced Common Murres (facial score 4) collected on Monterey Bay. From top to bottom, CAS 15788 (formative plumage, 25 October 1909), CAS 15792 (basic plumage, 15 October 1909), CAS 16071 (basic plumage, 26 November 1909), and CAS 16078 (basic plumage, 22 November 1909). Left, side view, and right, ventral view of the same specimens. Bill-width measurements indicated that 15792 and 16071 were in second basic plumage, whereas 16078 was an older bird. The extent of white in the secondaries (see Figure 2) in these four specimens was absent, thin, thin, and absent, respectively.

1.27 for facial score 2 (n = 23), 1.50 for facial score 3 (n = 14), and 2.78 for facial score 4 (n = 9), indicating that murres with darker faces also showed less white in the secondaries (linear regression, $P < 0.001$). The mean secondary score for birds with facial score 4 was also significantly greater than those of each of the other three groups (ANOVA, $P < 0.001$), while secondary scores of the other three groups did not differ from each other ($P > 0.098$). Most basic-plumaged murres with facial scores of 1 through 3 showed wide or moderate white secondary tips (only one specimen in each class showed thin tips), whereas of 8 murres with facial score 4, none showed wide white tips, four showed moderate tips, two showed thin tips, and two showed no white tips (CAS 15978 and 16078; Figure 4; see also lower photo on outside and upper photo on inside of this issue's back cover). Similarly, formative-plumaged murres with facial scores 1 through 3 all had wide or moderate white tips to the secondaries, whereas the one specimen with a facial score of 4 (CAS 15788) showed no white in the secondaries (Figure 4). Specimens of murres with a facial score of 4 also appeared to average darker in the flanks and underwing coverts than did those of scores 1 to 3 (Figures 1 and 4; images on inside and outside back cover), but I did not quantify these characters.

Eight basic-plumaged specimens and one formative-plumaged specimen

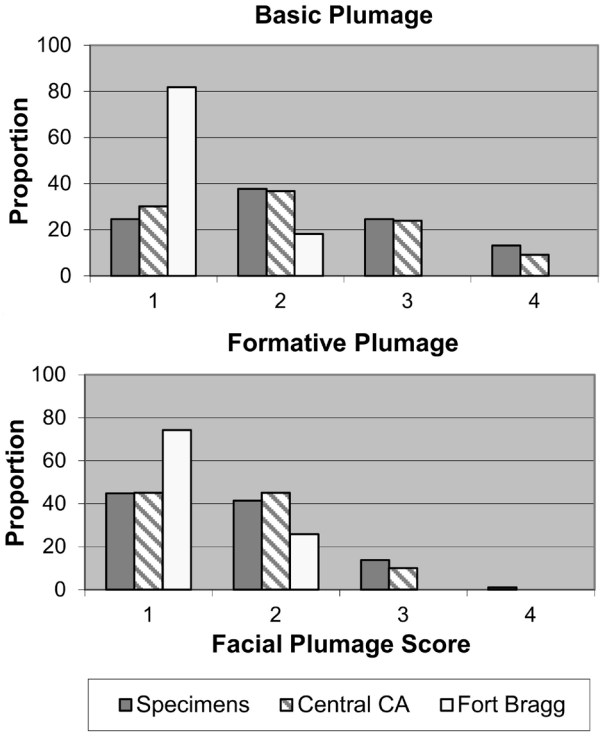

Figure 5. Distribution of facial scores (see Figure 1) of Common Murres in basic and formative plumage on the basis of specimens and birds studied in the field. The latter were scored between 30 September and 6 November, when birds should have few or no alternate feathers (see text). Birds observed on four trips from Bodega Bay to Half Moon Bay (30 September–6 November, 2011 and 2012) and on one trip off Fort Bragg (6 November 2011) analyzed separately. See text for statistical comparisons. Sample sizes for basic plumage: 61 specimens, 209 live birds off central California, and 55 live birds off Fort Bragg; for formative plumage: 29 specimens, 100 live birds off central California, and 31 live birds off Fort Bragg.

received a facial score of 4 (Figure 4), representing 13% of basic-plumage specimens and 3% of formative-plumaged specimens. On the four field trips off central California between 30 September and 6 November, 19 of the 209 (9%) basic-plumaged birds but none of the 100 formative-plumaged birds scored had dark faces. By bill width, five of the eight (63%) dark-faced specimens in basic plumage were in their second cycle (cf. Figure 4), whereas only 19 of 58 (33%) birds with facial scores 1 to 3 were in their second cycle; overall, faces were significantly darker in second-cycle birds (mean 2.63) than in older birds (mean 2.03; ANOVA, $P = 0.019$). A dark-faced bird in basic plumage photographed in Monterey Bay 15 September 2012 (inside back cover, top image) appears to have a medium-small bill, also sug-

gesting a second-cycle bird. On the other hand, another dark-faced adult, photographed 2 October 2012 off Half Moon Bay (inside back cover, bottom photograph) had a large bill and was attended by a young bird in formative plumage, suggesting it was a male at least four years of age, on the basis of minimum age at first breeding (Gaston and Jones 1998, Ainley et al. 2002); breeding males rather than females attend their young after fledging. Finally, of 33 specimens of juvenile murres at CAS and MVZ, three (9%) showed dark faces, while all five murres collected as chicks showed dark natal down in the face (Figure 6), corresponding to descriptions of the natal down of Common Murre (Gaston and Jones 1998, Ainley et al. 2002).

DISCUSSION

On the basis of this study, dark-faced and partially dark-faced Common Murres collected and observed off central California (Bodega to Monterey bays) during the fall may be completing their prebasic molt (September), initiating their prealternate molt (November), or in full basic or formative plumage (September through November). Of murres in full basic or formative plumage, most have white or mostly white faces. A small proportion, however, perhaps 10–15% of those in basic plumage and <5% of those in formative plumage, have mostly dark faces. Many of these also have little or

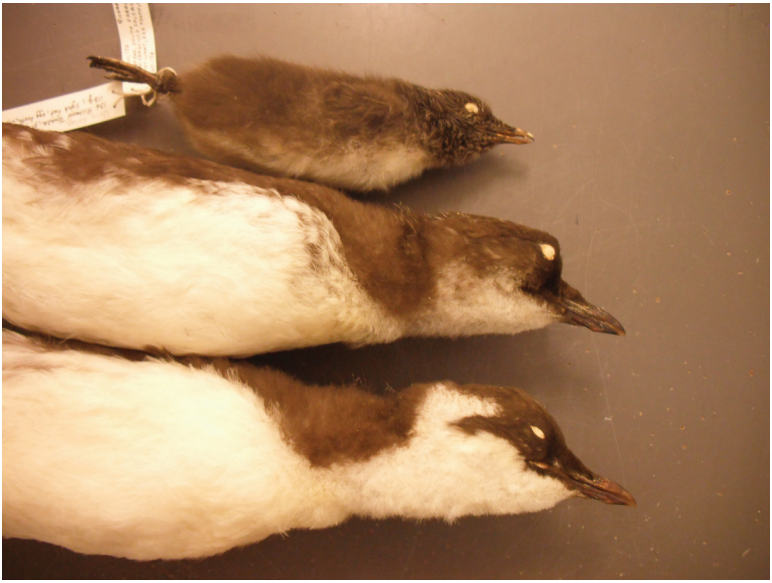

Figure 6. Variation in the head plumage of chicks and juveniles of the Common Murre. The nestling (top, CAS 88095) was collected on Southeast Farallon Island 7 June 1964; the juveniles (middle, CAS 15545; bottom, 15546) were collected on Monterey Bay 19 August 1909. CAS 88095 shows the pattern typical of natal down; CAS 15545 was one of only three of the sample of 33 juveniles showing dark auriculars.

Figure 7. Completely dark Common Murre with two in typical alternate plumage, photographed 24 July 2013, 14 km southeast of the Farallon Islands, flying south. That the dark bird was carrying a fish indicates it was breeding, perhaps on the Farallon Islands.

Photo by Dru Devlin NOAA/ONMS/ACCESS

no white on the trailing edge of the secondaries and appear to have darker underparts. Field observers should beware that such dark-faced birds can be confused with Thick-billed Murres. The distribution of dark and white in the face and secondaries suggests that the mechanisms resulting in the darkest-faced birds (facial score 4) may be different than those that result in the whiter-faced categories (facial scores 1 to 3).

Dark formative or basic feathering in the faces of Common Murres could result from asynchrony of the cycles of molt and deposition of melanin in the growing feathers. When a molt is early or late relative to the hormone cycle that signals pigment deposition, the resulting feathers may resemble those associated with earlier or later plumages (Pyle 1997, 2008, Howell 2010). Common Murres undergoing prebasic molt early, for example, might begin replacing feathers before hormone signaling switches the color from dark to white. Such birds might be expected to show more dark in the nape and auriculars and more white in the chin and throat, since within a molt dorsal head feathers are often replaced prior to ventral feathers (Pyle 2008).

The darkest-faced murres (facial score 4) showed such a pattern, having completely or largely dark napes and auricular regions and whiter chins and throats (Figure 4; photos on inside and lower outside of back cover), suggesting that they initiated their prebasic molt early, before hormone signaling had switched from dark to white. A similar mechanism may result in reduced or no white tips to the secondaries and darker underparts and underwing coverts in these birds. Being unconstrained by breeding, one-year-old alcids typically undergo the second prebasic molt earlier than older birds undergo subsequent prebasic molts (Pyle 2009), and this difference might account for the high proportion of darker-faced second-cycle birds I observed. For

example, the one-year-old murres collected 16 May (MVZ 145340 and MVZ 69) appeared to be undergoing early second prebasic molts that would have resulted in facial scores of 4 (Figure 3A and B). Older birds with darker faces (Figure 4) may represent 2- to 4-year-olds that had not bred yet or breeders that failed early the previous year, which could result in earlier prebasic molt. Possibly, this pattern of pigmentation extends to nestlings and chicks, resulting in darker-faced downy chicks and juveniles that hatched early (Figure 6). Some breeding birds also appear to show dark faces (lower inside back cover); another possible explanation for dark faces in these and other birds might be a later-than-normal signal for deposition of melanin imposed upon typical timing of prebasic molt. Although Ainley et al. (2002) reported females to molt earlier than males, I found only a slight and nonsignificant trend for females to show faces darker than those of males.

Murres undergoing a late prebasic molt, on the other hand, might start acquiring partially dark faces as hormonal signaling switches back to producing feathers typical of alternate plumage. Because molt of ventral tracts is later (see above), these birds might show white napes and auricular regions but partially dark chins and throats. Most murres of intermediate categories (facial scores 2 or 3) showed this pattern (Figure 1), indicating they may have undergone a late prebasic or preformative molt the previous fall, and/or that hormone signaling for dark feathers may have been early. Likewise, an early prealternate molt, before hormone signaling had fully switched to dark, might produce white in the faces, as shown by the two specimens with white-tipped alternate feathers (Figure 3C and D).

That early-replaced basic feathers appeared to be white with dark tips, and early-replaced alternate feathers dark with white tips, suggests that hormone signaling can switch quickly, as feathers are growing, as also suggested by such patterns in some ducks and ptarmigan (Pyle 2005, 2007), although some murres with facial scores 2 and 3 also appeared to have dark-tipped white throat feathers (Figure 1), opposite of what might be expected from a late prebasic or preformative molt. If asynchrony of the hormones stimulating molt and melanin deposition does explain variation in the patterns of the Common Murre's face, these results suggest that the signaling cycle produces dark-tipped white facial feathers in May and June, white facial feathers from July through September, white-tipped dark or dark-tipped white feathers in October, and dark feathers from November through April, although individual and age-related variation in the timing of this signaling is likely. If these interactions extend to the natal period, it could explain the dark faces developed by downy chicks in May and June and the dark faces of some early-hatched juveniles that may undergo the prejuvenal molt in early June. The precise timing and mechanisms of birds' pigment-deposition cycles are largely unknown and in need of further study.

Alternatively, the darkest-faced murres in formative and basic plumage could represent a polymorphism rather than asynchrony of pigmentation and molt cycles (cf. Sibley 2000:243). I examined or observed few murres intermediate between the whiter-faced categories (facial scores 1 through 3) and darkest-faced category (facial score 4). In both basic and formative plumage only the darkest-faced birds lacked white on the tips of the secondaries, and these birds also appeared to show more dark in the underparts and

underwing coverts. The single dark-faced specimen in formative plumage (Figure 4) is difficult to explain by the hypothesis of asynchronous hormone signaling and molt cycles. A completely dark individual was collected near the Farallon Islands on 30 May 1911 (CAS 18072; Figure 3E and F), and another was photographed 24 July 2013 near the Farallon Islands (Figure 7). Presumably these two birds represent hypermelanism.

However, the incidence of dark faces in central California in fall, 9–15% of basic-plumaged murres, is greater than typically attributable to a plumage abnormality such as complete or partial hypermelanism, and murres breeding farther north appear to show less dark in the face in general (see below). These observations suggest that asynchrony of the hormone signaling and molt cycles rather than polymorphism likely accounts for most or all dark-faced Common Murres in basic plumage off central California. Completely dark plumage, as seen in Figures 3E and F and Figure 7, also could result from extreme asynchrony of hormone cycles producing completely dark underparts during the previous prebasic molt, coupled with dark head feathering from the prealternate molt. In this regard, it is interesting that the darkest-faced birds also had darker basic feathers elsewhere, suggesting that signaling for dark feathers in birds undergoing early prebasic molt affects not just the head feathers replaced during the prealternate molt.

In summary, outgoing and incoming alternate feathers, and early-replaced and late-replaced basic feathers, all may contribute to the occurrence of dark-faced Common Murres off central California from September through November, as may hypermelanism in a small proportion of individuals. The lack of dark-faced murres observed off Fort Bragg on one pelagic field trip (6 November 2011) suggests the murres in that area may have come from other breeding populations, such as those in Mendocino, Humboldt, and Del Norte counties, northern California (Carter et al. 1992, Manuwal et al. 2001). At the largest of these colonies, on Castle Rock, Del Norte County, breeding appears to occur three weeks to a month later than at Southeast Farallon Island (R. Golightly and C. Strong pers. comm., Manuwal et al. 2001). The later breeding could result in later second and definitive prebasic molts, bringing molt into closer synchrony with the hormone cycle signaling for a white face. Further study of the complex interaction between molts and feather coloration of the Common and Thick-billed murres throughout their breeding ranges is needed for an understanding of geographic variation in facial plumages, and whether the cycles' interactions are influenced more by genetic or environmental factors.

ACKNOWLEDGMENTS

I thank Maureen Flannery (California Academy of Sciences) and Carla Cicero (Museum of Vertebrate Zoology) for assistance and access to specimens, Debi Shearwater for invitations to lead pelagic field trips for Shearwater Journeys, Rick Golightly and Craig Strong for information on the Castle Rock murre colony, and Alan Wight, Al Jaramillo, and Dru Devlin for use of their photographs. Jeff N. Davis, Ian Jones, Al Jaramillo, and Steve N. G. Howell reviewed the manuscript or provided feedback on murre plumages. I am forever indebted to Rollo Beck, who collected and prepared the great majority of specimens examined for this study. This is publication 463 of the Institute for Bird Populations.

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Outside back cover: Common Murres over Cordell Bank off Bodega Bay, California, 7 October 2012, showing variation in head plumage. Note also the white trailing edge to the secondaries on the whiter-faced bird (upper image), lacking on the darker-faced bird (lower image). Both birds are in full basic plumage. *Photos by Alan Wight*

Inside back cover (upper): Common Murre, Monterey Bay, California, 15 September 2012. This individual shows a particularly dark face. Note also the lack of white on the trailing edge of the secondaries. The medium-small bill suggests that it is a second-cycle bird. *Photo by Alvaro Jaramillo*

Inside back cover (lower): Common Murres off Half Moon Bay, California, 2 October 2011. The chick appeared to be attending this dark-faced adult, suggesting the latter was a male at least four years of age. *Photo by Peter Pyle*