Sunset Sanderlings

Digital photography leads to novel insights about the presupplemental molt of the Sanderling

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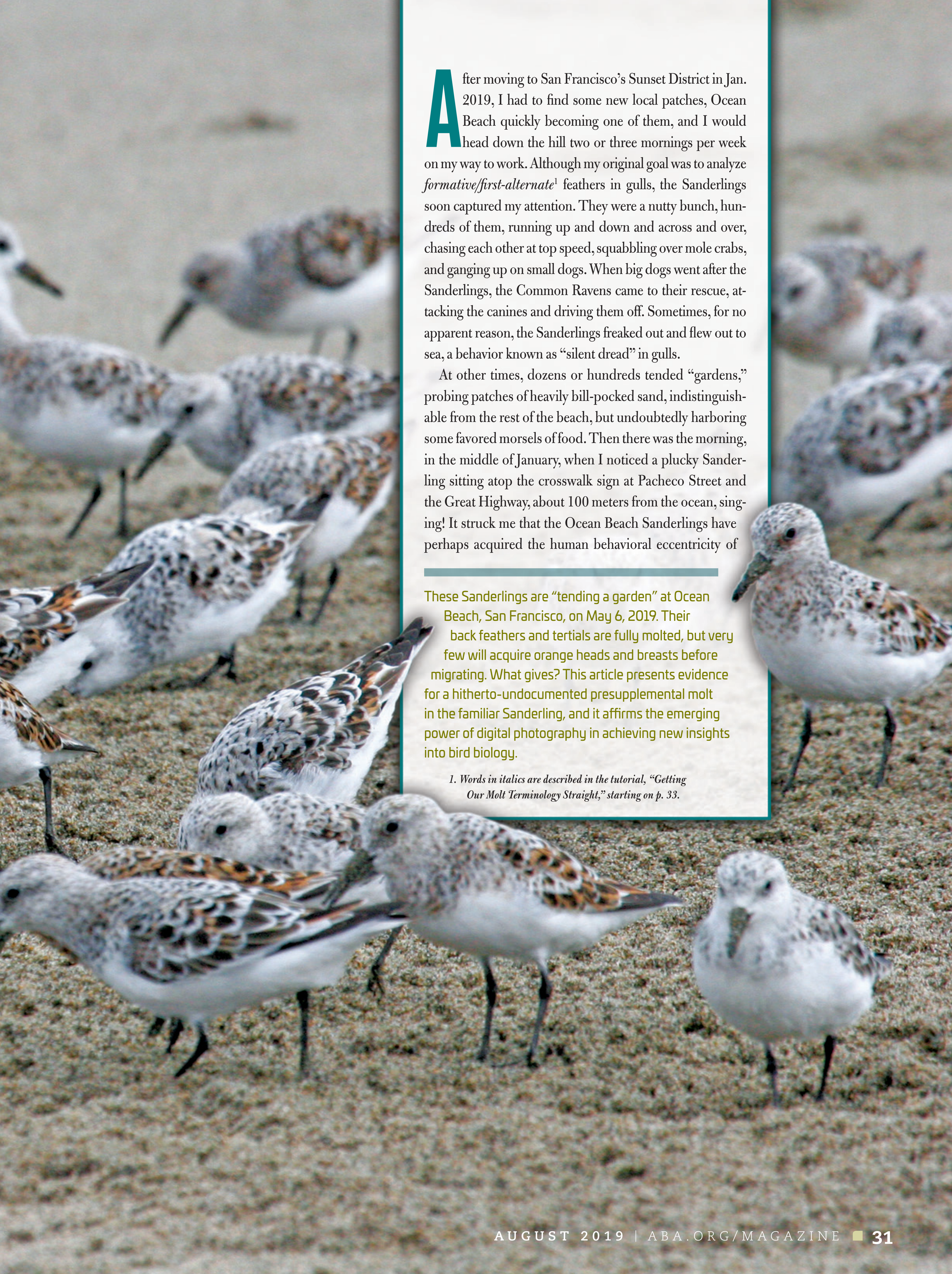
NOTE: All live Sanderling photos in this article are from the spring of 2019 at Ocean Beach or Fort Funston Beach, San Francisco, California. Except for Fig. 8, all photographs and figures by © Peter Pyle. This is publication #628 of The Institute for Bird Populations.



After moving to San Francisco's Sunset District in Jan. 2019, I had to find some new local patches, Ocean Beach quickly becoming one of them, and I would head down the hill two or three mornings per week on my way to work. Although my original goal was to analyze *formative/first-alternate*[1] feathers in gulls, the Sanderlings soon captured my attention. They were a nutty bunch, hundreds of them, running up and down and across and over, chasing each other at top speed, squabbling over mole crabs, and ganging up on small dogs. When big dogs went after the Sanderlings, the Common Ravens came to their rescue, attacking the canines and driving them off. Sometimes, for no apparent reason, the Sanderlings freaked out and flew out to sea, a behavior known as "silent dread" in gulls.

At other times, dozens or hundreds tended "gardens," probing patches of heavily bill-pocked sand, indistinguishable from the rest of the beach, but undoubtedly harboring some favored morsels of food. Then there was the morning, in the middle of January, when I noticed a plucky Sanderling sitting atop the crosswalk sign at Pacheco Street and the Great Highway, about 100 meters from the ocean, singing! It struck me that the Ocean Beach Sanderlings have perhaps acquired the human behavioral eccentricity of

These Sanderlings are "tending a garden" at Ocean Beach, San Francisco, on May 6, 2019. Their back feathers and tertials are fully molted, but very few will acquire orange heads and breasts before migrating. What gives? This article presents evidence for a hitherto-undocumented presupplemental molt in the familiar Sanderling, and it affirms the emerging power of digital photography in achieving new insights into bird biology.

1. Words in italics are described in the tutorial, "Getting Our Molt Terminology Straight," starting on p. 33.

the area. Or, given the chronology of it, maybe the Ocean Beach humans have acquired Sanderling idiosyncrasies.

From January to mid-March, all of the Sanderlings were in full winter, mostly white, *formative* or *basic* plumage. I started thinking ahead to April and May, when they would be in *alternate* plumage, all showing the bright orange heads and breasts of breeding appearance. But wait a minute. It struck me that I'd never seen a bunch of bright orange-headed Sanderlings evading the waves in central California. Many return in July and August in worn orange feathering, but I couldn't recall a pack of bright birds in spring. Do they maybe head north from this area before acquiring fresh alternate plumage? Hmm.

The molt and plumage strategies of some of our most common birds continue to elude us. Where do Indigo Buntings undergo the complete *prebasic* molt? How many *inserted first-cycle* molts do our large white-headed gulls have? Did the bright alternate plumage of male American Goldfinches evolve to attract females, or did the *prealternate* molt evolve for other reasons, to then be co-opted by the males? Sanderlings are common birds, but how well do we really know their prealternate molt? Digital camera at my hip, I decided to make like the Sanderlings myself, and do a bit of probing.

Setting the Stage

Ocean Beach extends roughly 3.4 miles (5.5 kilometers), from the famous Sutro Baths and Cliff House southward to the foot of Sloat Boulevard, near the San Francisco Zoo. The beach's heyday was in the 1920s–1960s, before Sutro burned down and became an abandoned, cement-lined wetland; the Art Deco amusement park Playland At The Beach to the south was torn down to make room for ugly condominiums, and the grand Fleishhacker Pool, birthplace of Ocean Beach surfing, became a parking lot for the zoo. Ocean Beach is run down now, with cement walls cracking, floodwaters and sand covering the highway, old sewer outfalls plugged up, garbage cans overflowing, and off-leash dogs and scrounging ravens scampering among joggers, surfers, nonconformists, and eastern European tourists wearing inflatable lobster swimming-pool rings. Bonfires rage at night, harkening the days before the "Burning Man" annual techno-art phenomenon relocated from Ocean Beach to the high desert of Nevada. Despite all of this, the gulls, Sanderlings, Whimbrels, and, surprisingly, a stalwart group of wintering Snowy Plovers seem right at home.

When time permitted, I stopped at three or four vantages to scan and survey the beach. From Jan. to early May of 2019, beach-wide numbers of Sanderlings ranged from about 400 to 1,200, the variation apparently reflecting tide-influenced movements to and from Fort Funston Beach, which also can host hundreds of wintering Sanderlings at lower tides. There may have been added northbound migrants pit-stopping in May. In any case, numbers were more than sufficient for my inquiry.

Variable Sanderling Molt and Appearance

The first sign of *prealternate molt* came on Mar. 20, when I observed two Sanderlings, among a flock of 30, that had dropped a scapular or two. That this was molt and not just accidental feather loss was confirmed on Mar. 31, when about 25% of the Sanderlings had dropped these same and other scapulars, as well as their middle *tertials*, the gaps filling with incoming feathers (Fig. 1). To my surprise, these new

Fig. 1. This **Sanderling** is molting the scapulars and tertials on Mar. 31, 2019. Note that the incoming, dark-centered feathers lack rufous, instead being fringed grayish white.

Fig. 2. By Apr. 15, an estimated 80% of **Sanderlings** showed upperpart-feather replacement, but little to no rufous among the new back feathers and no orange to the head or breast.

Fig. 1

Fig. 2

feathers had little to no rufous or orange, their large black centers fringed broadly with grayish white. By Apr. 15, an estimated 80% of the birds showed upperpart-feather replacement, with the most advanced of these replacing most or all upperpart feathers along with all three tertials (Fig. 2). Although a few tinges of rufous could be seen, it was not until Apr. 26 that extensive rufous became evident in the back-feather fringing (Fig. 3a), the most advanced birds also gaining some orange feathering to the crown, head, and breast (Fig. 3b). More than 90% of the Sanderlings during Apr. 26–May 6, however, remained white on the head and breast (Fig. 4). A few showed orange patches here, and only about one in 50 (of 1,200) were close to "full breeding appearance" on the latter date (Fig. 5). Appearance of upperparts and underparts was otherwise variable, with most birds showing fully replaced back feathering but breasts that were white or white with indistinct black markings (Figs. 6a–d).

During early May, a large proportion of birds departed, with numbers dropping from 1,000–1,200 Sanderlings on May 6 to 200–400 by May 9. The amount of red and orange in the feathering similarly dropped: On both May 11 and May 14, I could find, at most, only one orange-headed bird among about 350 remaining Sanderlings, a substantial proportion continuing to lack orange on the heads and breasts. These included many first-cycle birds that I studied and photographed (Fig. 7a), but also quite a few older birds (Fig. 7b). Numbers continued to decrease: 42 on May 18, none between May 20 and May 25, then 53 on May 26, 15 on May 31, and the last four noted on June 2. Perhaps these later birds represented passage migrants; in any case, as is typical at these northern latitudes, we rarely if ever see any oversummering Sanderlings in central California. All birds studied May 14–18 were completely white-headed, and many if not all appeared to be first-spring birds; in contrast, about 20% of the birds on May 26 were fully orange-headed, as were two of the four on June 2.

Up to this point, I had not consulted the primary literature on this topic, although I knew of several good studies and summaries on Sanderling molt (Chapman 1896, Stone 1897, Dwight 1900, Dement'ev and Gladkov 1951, Cramp and Simmons 1983, Myers et al. 1985, Higgins and Davies 1996, MacWhirter et al. 2002), including one of my own (Pyle 2008), in which I could not recall details of Sanderling molt. I was also aware of studies on Bar-tailed Godwits (Piersma and Jukema 1993, Conklin and Battley 2011), Ruffs (Jukema and Piersma 2000), and Great Knots (Battley et al. 2005) reporting two *inserted molts* in spring, one on the wintering grounds and another at stopover locations on the way to the breeding grounds. Might Sanderlings also have two inserted spring molts?

Fig. 3. It was not until Apr. 26 that extensive rufous became evident in the back-feather fringing of the San Francisco **Sanderlings.** The individuals shown here were notable in having undergone more extensive upperpart-feather molt than most (Fig. 3a), and in showing by far the most orange on the head and breast (Fig. 3b), of 550 Sanderlings observed on Fort Funston Beach. Almost all (>95%) Sanderlings on this date lacked orange on the head and breast (compare with Fig. 4).

Getting Our Molt Terminology Straight

Lately I have been encouraging birders to fully adopt Humphrey and Parkes (1959) or "H–P," nomenclature, as revised by Howell et al. (2003). Having been immersed, at times drowning, in molt and plumage investigations for nearly 40 years now, there is no question in my mind that the revised H–P system far exceeds previous terminologies in its elegance and accuracy, as well as in serving as a platform for teaching molt and furthering our understanding and investigation in the field. Some consider H–P too overwhelming for birders, clinging to confusing molt and plumage terminologies related to season, location, breeding phenology, and/or plumage coloration. But I prefer to push envelopes, and I'm encouraged to see younger birders, at least, "getting" and successfully embracing H–P. A critical step in understanding the H–P system, one that still evades many H–P protagonists, is that the terminology is based not on present-day (flattened) molt timing or

Fig. 4

Fig. 4. This group of **Sanderlings,** on May 6, were well along in, or had completed, upper-part-feather molt but still retained largely to entirely white heads and breasts. Completing molt of back feathers before replacing any head and breast feathers is not how body-feather molting occurs in the well-studied Bar-tailed Godwit (Conklin and Battley 2011) or how it usually proceeds in other birds.

feather coloration, the case with all antediluvian terminologies, but on the history, or evolution, of molts along a taxonomic lineage. Once this is grasped, everything falls pleasingly into place.

The complete or nearly complete *prebasic molt,* occurring on an essentially annual cycle in all birds, is part of a physical restoration process that has evolved from similar processes (including ecdysis, or epidermal molt) in reptiles, and probably the ancestors of reptiles as well. This restoration process fixes the H–P molt terminology, regardless of the timing or location of this molt. As ancient birds evolved from reptiles and then to modern-day avian taxa, certain feathers in certain species had to be replaced more than once per year, and *inserted molts* became established within the prebasic molt cycle. The first inserted molt to evolve within a definitive (mature-plumage, or "adult") prebasic molt cycle is termed the *definitive prealternate molt,* and, if a second inserted molt evolves, it is termed a *definitive presupplemental molt* (Pyle 2007). The first molt cycle differs from subsequent annual molt cycles in that an extra inserted molt has evolved, usually commencing within a few months of fledging. This is termed the *preformative molt* (Howell et al. 2003), and it is often (but not always) followed by a *first prealternate molt* in species that undergo definitive prealternate molts. In all cases, the molts produce the equivalently named plumages; for instance, the prealternate molt produces the alternate plumage. It is thus that molts—and not the ensuing plumage appearance—define H–P terminology. There are a few additional complexities in the world of bird molt, but the above captures what we need to know to evaluate our Ocean Beach Sanderlings.

Fig. 5. The **Sanderling** to the left, photographed on May 9, was the only one of about 350 that showed "full breeding appearance" on this date. The two birds to the right were more typical.

Fig. 5

Back to Our Sanderlings

Prealternate molts in Sanderlings have been reported to occur primarily on the wintering grounds but "can complete on breeding grounds or at stopover sites" (Pyle 2008). In many shorebirds, the first prealternate molt is generally less complete than the definitive prealternate molt, resulting in a "less-full breeding appearance," especially for first-cycle shorebirds that over-summer on the wintering grounds. However, a less-full appearance can also depend on when a feather gets replaced relative to pigment-deposition cycles (see Pyle 2008, Pyle 2013, Howell 2010). For example, alternate feathers developed earlier or later relative to pigmentation cycles in shorebirds can produce feather colors and patterns that fall short of peak breeding appearance. For this reason, a less-full breeding appearance does not necessarily result from a less-complete prealternate molt, and it may not be confined to yearling breeders.

Most birds molt body feathers more-or-less "from head to toe," both above (dorsally) and below (ventrally), so it seemed unusual to me that upperpart feathers in the Ocean Beach Sanderlings were so thoroughly replaced while head and breast feathers on most birds remained unmolted. Might the head and breast feathers molt from white basic to white alternate feathers in March–May on the wintering grounds, to be replaced again by orange supplemental feathers at stopover locations?—for example, the saline lakes in the Canadian prairies (see Macwhirter et al. 2002). This is essentially the strategy reported for Bar-tailed Godwits and Great Knots.

Or might it be that individual differences in breeding appearance result from variable timing of feather replacement relative to pigment-deposition cycles during a single protracted or suspended molt? In other words, is it possible that, within a single molt (each feather follicle activated only once), replaced feathers come in white, then white with dark flecking, and then orange as the molt progresses and the birds move from the wintering grounds to stopover locations to the breeding grounds, resulting in an overall orange appearance to the head and breast, despite the presence of scattered, earlier-replaced, white feathers (Pyle 2008, Howell 2010)? Documenting which of these two scenarios (or both!) occurs in birds has been a challenge, best accomplished by following individuals to see how often feather follicles activate, as Conklin and Battley (2011) were nicely able to do with radio-tracked Bar-tailed Godwits. But we can also make some inferences from dedicated fieldwork and specimen examination.

Rollo Beck to the Rescue

Here in the 21st century, avian specimen collections continue to be an underutilized resource for studies of identification, molts, and plum-

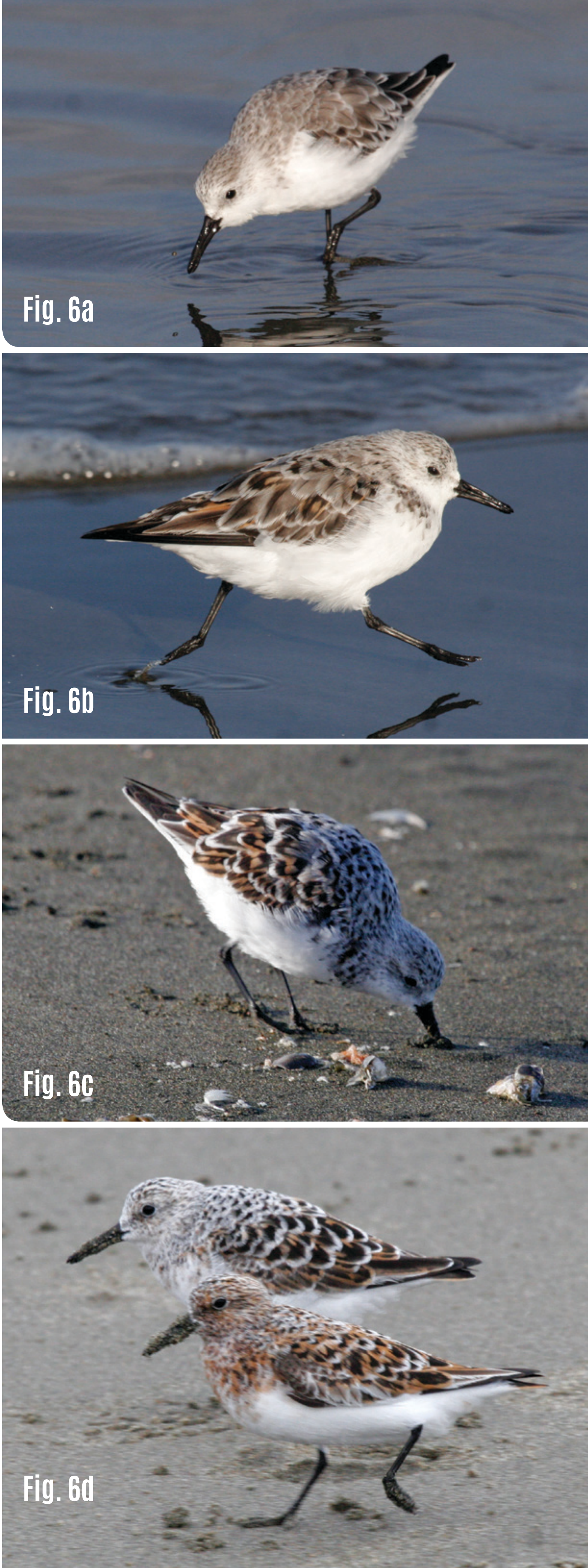


Fig. 6. These images depict variation in the molt progress and appearance of **Sanderlings** on Ocean Beach, on May 1 (Figs. 6a–c) and May 6 (Fig. 6d), 2019. Both upperpart and underpart coloration varied substantially, but not necessarily in concert with each other.

ages, and I still don't understand why. Are birders worried about the chemicals used to preserve bird skins? That's a reasonable apprehension these days, especially to those who are sensitive to chemicals, but in my experience this does not include too many birders. Is it too heady? Too academic? Are the collection managers scary? I suspect that one or more of these issues may affect some birders who would otherwise benefit greatly from this incredible resource. Whatever the reason, I encourage more birders to give these collections a spin, supporting their continued curation in the process. Believe me, the curators are not interested in adding you to their collections! In any event, to make things easier, many museums are creating digital 3D images of their specimens, enabling online study, increasingly via virtual reality; go online to see the Slater Museum of Natural History's pioneering efforts in this regard (tinyurl.com/Slater-digital-birds).

To probe deeper into my questions on Sanderling prealternate molt, I consulted the 354 skins housed at the California Academy of Sciences, San Francisco (now a 12-minute bike ride away), and the Museum of Vertebrate Zoology at the University of California at Berkeley. As with other waterbird species, many—and somehow the most important—specimens in these collections were collected by the indefatigable Rollo Beck (Fig. 8; see Pyle 2008, Pyle and Reid 2016). Beck spent over 50 years, from the 1890s to 1950, collecting seabirds throughout the Pacific region, and also procured thousands of waterbirds in central California, primarily around Monterey Bay, foraging for specimens from his inland ranches and farms at Los Gatos and Planada. Among the 354 specimens of Sanderlings at these two collections, 71 were collected in the process of spring molt in California, 24 by Beck. Kudos also to Harry S. Swarth, E. W. Gifford, and E. W. Martin for their contributions.

These 71 California specimens were collected between Apr. 10 and June 2. For each one, I assessed the presence or absence of breast-feather molt and I gave a score for overall breast color and pattern from 0 to 5, according to the specimens shown in Fig. 9. For comparison, I also scored all birds collected on the breed-

Fig. 8

Fig. 8. This is Rollo Beck, photographed by Edwin H. Bryan, on Wakaya-lailai Island, Fiji, Oct. 17, 1924, as part of the Whitney South Sea Expedition; they were cabin mates on the schooner *France*. Two of the least-known and most enigmatic Procellariiformes in the Pacific are named for these researchers, Beck's Petrel and Bryan's Shearwater.

Fig. 7. By mid-May, many remaining **Sanderlings** were first-cycle birds (Fig. 7a, May 9), showing retained juvenile wing coverts and pointed, brown outer primaries. There were also a lot of older birds (Fig. 7b, May 14), showing higher-quality definitive basic coverts and remiges. Surprisingly, specimen examination revealed no significant difference in breast coloration between the two age groups; if anything, younger birds averaged more orange to the head and breast than older birds among both those collected molting in California and those collected in "full breeding appearance."

Fig. 7a

Fig. 7b

Fig. 9. Scores for evaluating head and breast color in **Sanderling** specimens in this study ranged from fully white-breasted as in winter appearance (0), to marked dark with little or no orange (1, 2), to showing partial (3, 4) to "full" (5) breeding appearance. Specimens, all from the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley, were collected at Monterey Bay on Feb. 10, 1911 (0, MVZ 18979), May 2, 1940 (1, MVZ 90965), July 26, 1935 (2, MVZ 75068), and May 2, 1940 (3, MVZ 91546); at Barrow, Alaska, June 7, 1951 (4, MVZ 126737); and at Watsonville, California, May 17, 1940 (5, MVZ 87146). Examples of plumage variation include the adult collected in breeding appearance and showing no orange at all (score 2), and the adult collected in "full breeding appearance" in California as early as mid-May (score 5). Perhaps this latter specimen was selectively collected, as <1% of Ocean Beach birds had this appearance by this date; see text for details.

ing grounds on tundra in Alaska (*n*=16, May 27–June 14) and all adults collected south of the breeding grounds but prior to the molting of the innermost primary (p1) in late summer (*n*=17, July 16–Aug. 26); the individuals of this latter sample had not molted breast feathers yet and still retained their breeding appearance. I aged each bird as first-cycle or adult according to criteria in Pyle (2008), and I assumed the sex designations on specimen labels were correct.

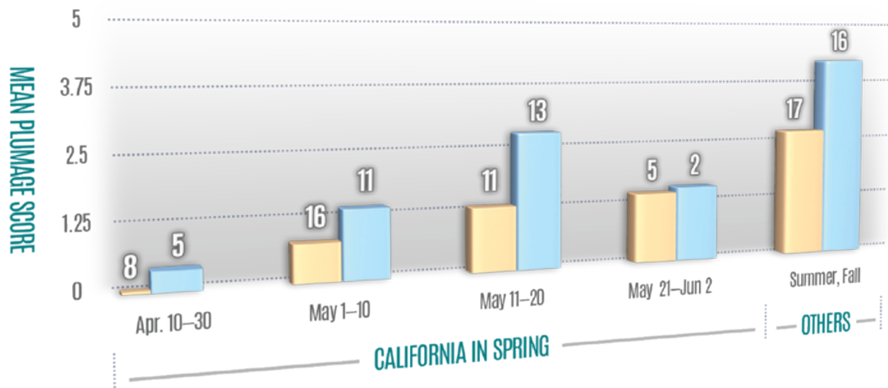
Within each sex, surprisingly, I found no significant differences between first-cycle birds and adults in breast-plumage scores. In fact, first-cycle Sanderlings showed slightly higher mean scores than adults, in both molting California birds and those in breeding appearance. Ages were therefore pooled for analysis. To assess the acquisition of orange breast feathering while molting, I separated the California-collected specimens into four temporal groups: Apr. 10–30, May 1–10, May 11–20, and May 21–June 2.

Males showed higher mean breast-appearance scores than females collected both in California and in breeding appearance (Fig. 10a), as has been previously reported (Pyle 2008). For both sexes, birds collected in breeding appearance showed substantially higher scores for overall breast color and pattern than those molting in California, indicating further molt following departure from California. Many, if not most or all, specimens collected early during the molting period had incoming breast feathers that were white or white with dark marks (Fig. 10b), whereas those found molting later (Fig. 10c) showed incoming orange feathers, in many cases appearing to replace white or marked feathers from the first inserted molt.

I admittedly didn't track individuals for follicle activation, but I consider the photographic and specimen record to be strong evidence that Sanderlings undergo two inserted molts between late March and mid-June. Thus, they undergo a presupplemental molt. Whether replaced during the first or the second molt, new feathers generally emerged white during March and April, spotted or marked dark in late April and May, and orange in mid-May and June, but with a lot of individual differences that reflect the independence of molt and plumage-deposition cycles (Fig. 11; see Pyle 2013). As with Bar-tailed Godwits, the molt in Sanderlings of most to all head and breast feathers occurs concurrently with that of most to all upperpart feathers in late March through April or early May, with the evidence indicating a second replacement, of head and breast feathers at least, in May–June (Fig. 11). As first-cycle Sanderlings seem also to show this molt strategy, it means three inserted molts, including a *first presupplemental molt,* occur within the first molt cycle of this species, rarely documented in birds. (On a technical note, we have disregarded the molt formerly termed "first presupplemental," which is now called "auxiliary preformative"; see Thompson and Leu 1994, Howell et al. 2003, Pyle 2008). Assuming this scenario really happens, where does one inserted spring molt stop and another start? And how do we sort it out in H–P terms?

Ignore Feather Color!

Conklin and Battley (2011) did a reasonable job discussing the two inserted spring molts of Bar-tailed Godwits in H–P terms, considering how these molts may have evolved (see also Battley et al. 2005). In Conklin and Bat-



Numbers above bars are sample sizes.

Fig. 10a

Fig. 10b

Fig. 10c

tley's godwits, unmarked breast, side, and flank feathers are largely replaced by barred feathers on the wintering grounds in New Zealand, and these can be replaced again by rufous feathers in New Zealand and at stopover locations, including the Yellow Sea region between China and Korea. But, as with Sanderlings, there is generous variation in molt timing and resulting feather color, both according to sex and among individuals within each sex. Conklin and Battley surmised that the initial molt on the wintering grounds was the prealternate molt, as with many other shorebirds, and that the second replacement evolved later and should be considered the presupplemental molt. This is logical, and may well be correct, but I have different ideas about a couple of their conclusions.

First, Conklin and Battley defined feather generation based on plumage color. They considered barred feathers alternate and rufous feathers supplemental, and, due to the variable extent of both molts, they surmised that rufous supplemental feathers could replace either pale basic feathers or barred alternate feathers. A molt's replacing two previous generations of feathers is acceptable under H–P; this occurs in first-cycle individuals in such birds as Franklin's Gulls, Indigo Buntings, and Bobolinks, which undergo relatively extensive first prealternate molts to replace both juvenile and formative feathers of formative plumage. However, defining the generation based solely on feather

Fig. 10. The graph (Fig. 10a) summarizes mean breast-appearance scores (compare with Fig. 9) for (1) Sanderlings collected in California during four temporal periods encompassing molt and (2) Sanderlings in breeding appearance collected on the breeding grounds or during southbound migration following breeding. Sample sizes are noted above bars. Surprisingly, mean scores did not correlate significantly with age, but males consistently averaged more orange on the breast than females. In both sexes, the substantially higher scores of specimens collected in breeding appearance compared to those collected during the molting period in California indicate further molt into orange feathering after leaving the wintering grounds in the state.

The drop in scores during the last period of May appears to reflect earlier departure of birds with more orange plumage. Plumages vary greatly among individual birds, however—standard deviations around these means are large—with some individuals gaining plumage score 5 in California (compare with Fig. 9, score 5) and others showing little or no orange to the breast in breeding appearance (compare with Fig. 9, score 2). By closely examining specimens, we see that birds collected in April and early May (for example, California Academy of Sciences specimen 74405, from Pescadero Lagoon, May 8, 1937) are undergoing molt and show mixed worn white basic feathering, as well as newly replaced feathers that are white or white with dark markings (Fig. 10b). Inserted (alternate) feathers are typically more filamentous than basic feathers, as they are usually only needed for a few months and the "fluffiness" can enhance the display appearance, if this is the function of the inserted plumage.

However, birds collected in late May at stopover locations in Canada (for example MVZ 75528 collected at Gimli, Manitoba, May 29, 1920) along with several other specimens at the Museum of Vertebrate Zoology collected at Beaverhill Lake, Alberta, were molting breast feathers and were replacing dark-marked white feathers with orange feathers (Fig. 10c). The results shown in this figure suggest that Sanderlings undergo two inserted molts in spring.

color is not acceptable. Rather, I like to pretend that the birds are entirely black, like the Ocean Beach ravens, and the molts are then defined by *replacement episodes*, perhaps best conceptualized in terms of bell-shaped curves (Fig. 11). The number of inserted molts overall is defined by the number of times at least some feathers are replaced, but each inserted molt is defined by the episode in which it occurs, irrespective of follicle-activation timing and location. The plumage is simply defined as what follows the molt episode, irrespective of how many feathers of what generation were replaced, how many generations resulted, and what pattern or color the ensuing feathers displayed.

Let's leave Sanderlings for a moment and think about the molts and plumages of the familiar American Goldfinch. By looking at feather color, a conclusion can be drawn that the prealternate molt in this species evolved for purposes of sexual selection, the bright yellow alternate feathers of males being the adaptive result. But what if we pretend American Goldfinches were entirely black in all plumages? We then focus simply on the molts, as dictated by H–P interpretation, and we realize that females also have a prealternate molt but don't change color. It then becomes easier to reach the conclusion—which I believe is correct—that the inserted prealternate molt in American Goldfinch evolved for reasons other than sexual selection, perhaps because body feathers in this open-country species become abraded with solar exposure and have to be replaced twice per year to keep them working well. Once the molt evolved, the males took advantage by acquiring bright yellow alternate feathering, which, along with their songs, attract females. (Although I suppose it's possible, I'm having trouble envisioning how a molt could evolve for reasons of an ensuing adaptive plumage color, when this color is not exhibited until the molt has evolved!) With the American Goldfinch, the pressure of sexual selection might have caused the prealternate molt in males to become more extensive than in females, but such an investigation is still needed in this common species.

The second cavil I have with Conklin and Battley is their presumption that the first inserted molt of Bar-tailed Godwits necessarily is prealternate and the second one presupplemental. It may seem natural to define these two molts chronologically within the prebasic molt cycle, although Humphrey and Parkes (1959) never directly addressed this question. In any event, as I mentioned earlier, these two molts may instead have to be defined in the order in which they evolved along a shorebird ancestral lineage (see Pyle 2007). This is, no doubt, difficult to know or even to guess at. Conklin and Battley were correct in comparing spring Bar-tailed Godwit molts with those of other shorebirds that presumably undergo only one inserted molt per year, and they understandably concluded that the first molt is best regarded

Fig. 11a • Definitive Molt Cycle

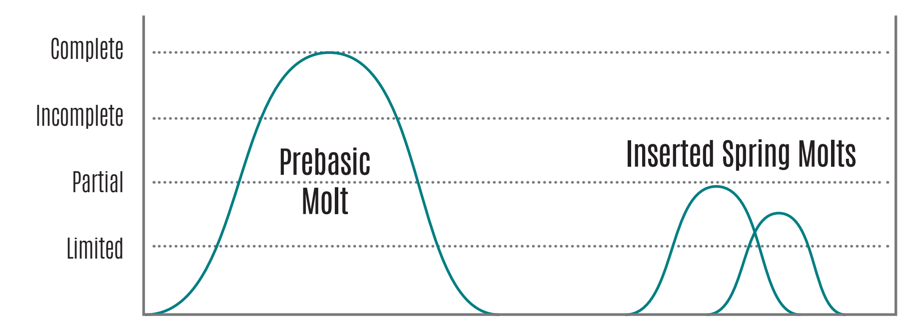


Fig. 11b • Color-deposition Cycles

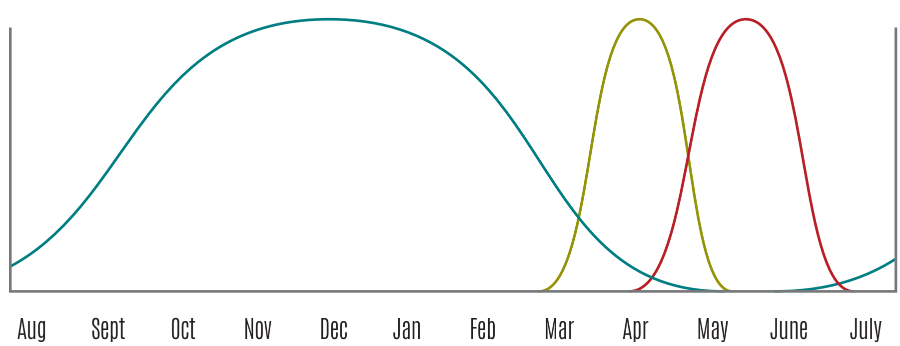


Fig. 11. In these diagrammatic representations of proposed molt (Fig. 11a) and proposed feather color deposition (Fig. 11b) cycles in Sanderlings, bell-shaped curves describe individual variation within the entire population. Color-deposition cycles are controlled by hormonal processes separate from those controlling molt. Thus, the two cycles appear to act independently within any particular individual bird, creating substantial variation in plumage patterns during spring and summer. For example, an individual Sanderling can find itself on opposite ends of the bell-shaped molt and plumage deposition curves, resulting in less-than-peak breeding-appearance coloration.

During the first inserted spring molt, feathers come in primarily white (blue curve) or white with dark markings (green curve). However, in the case of birds with more advanced color-deposition cycles, orange feathering (red curve) is acquired, resulting in "full breeding appearance" in California (compare with Figs. 5, 9). Likewise, birds molting during the second period develop more orange-colored feathers, although some with earlier molt or later deposition cycles can largely retain a winter appearance for breeding (Fig. 9). Each molt could begin on the wintering grounds, suspend for migration, and finish at stopover locations, creating even more individual variation!

as "homologous" with (sharing the same evolutionary origin as) the prealternate molts of other species. But do we know enough about shorebird molts to say that?

The presupplemental molts of shorebirds, including (apparently) the Sanderling, have thus far been discovered by noticing changes in plumage coloration. But, remember, we must ignore feather color! What if other shorebirds have two inserted molts but do not change color, which is perfectly expectable, as in the female American Goldfinch. We have little to no clue if, for example, the familiar Greater Yellowlegs has one or two inserted spring molts. American Golden-Plovers undergo spring migration from South America largely in winter appearance, to molt into breeding appearance at stopover locations in North America. We reflexively treat the molt in North America as the prealternate molt, but what if golden-plovers also have an inserted molt from plain feathering to plain feathering in South America, followed by a second inserted molt in North America? Would the second molt necessarily be prealternate? Can we really say which molt, and for what reasons, evolved first along an ancestral shorebird lineage? No, we're not there yet.

To get this right, we must go back to the molts of a common ancestor to godwits and Sanderlings, something perhaps shared with curlews or curlew-like taxa, according to at least one recent Scolopacid phylogeny (Gibson and Baker 2012). Alas, the prealternate molts of curlews are just as poorly known as any other shorebird (Pyle 2008), if not more so, mostly because color and pattern among all feather generations remain largely invariable. Even if we figure out curlew molts, there's no guarantee that the molts of Bar-tailed Godwits and Sanderlings are homologous with those of curlews or with each other, as a second inserted spring molt could have evolved independently in each ancestral lineage, or in a common ancestor that postdated the split from curlews. Further, how do we deal with geographic and intraspecific variation in molts and plumage coloration, as has been shown for Bar-tailed Godwits (Conklin and Battley 2011)? Sanderlings can display both "Northern Hemisphere" and "Southern Hemisphere" molting strategies (Pyle 2008: 500–505; Howell 2010), my spring 2019 investigations being of the former. How might the spring inserted molt strategies of these birds differ with those of Sanderlings that winter in South America? Sigh.

At times I feel good about our progress in understanding bird molt. But at other times the subject is enough to drive me a bit nutty, to run hither and yon in the Ocean Beach fog, and, perhaps, on a bad day, or maybe a good day, to sing the virtues of H–P nomenclature from atop a crosswalk post.

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