MOLT CYCLES AND SEQUENCES IN THE WESTERN GULL

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ABSTRACT: We describe the molt cycle of the Western Gull (*Larus occidentalis*) in central California on the basis of field observations of unmarked birds. The Western Gull has one partial and one complete molt per year. The first and second partial molts span up to 7 or 8 months, subsequent prealternate molts about 4 to 6 months. The complete prebasic molt spans 5–6 months. We propose that the Western Gull exemplifies a pattern more widespread among large water birds: the first partial ("postjuvenal") molt appears homologous with later prealternate molts, not with the prebasic molt, as considered previously.

The Western Gull (*Larus occidentalis*) is a locally common breeding species along the west coast of North America. Two subspecies are widely recognized (AOU 1957): nominate *occidentalis*, which breeds from Washington and perhaps southern British Columbia (Campbell et al. 1990) to central California, and the more southerly *wymani*, which breeds from central California south to central Baja California.

Despite the Western Gull's being large and conspicuous, its molt cycles and sequences are treated inadequately in the literature. Pierotti and Annett (1995) recently described the plumage sequences of the Western Gull. They based their account largely upon the seminal work of Dwight (1925), whom they considered the only author in North America to have tackled this complex subject, but they overlooked the important work of McCaskie (1983). For example, Pierotti and Annett (1995) limited the complete second prebasic molt of Western Gulls to August and September, while McCaskie gave July to October for this molt. Conversely, Pierotti and Good (1994) noted that the complete second prebasic molt of the Herring Gull (*L. argentatus*) takes a minimum of four months and usually as long as six, making it all the more surprising that the equally large Western Gull might require only two.

STUDY AREA AND METHODS

From January 1997 through May 1999 we made regular observations, in all months of the year, of Western Gulls at Bolinas Lagoon, Marin County, and Bodega Bay, Sonoma County. We used calendar years (CY) to avoid potential ambiguity in describing the age of a bird; thus, the bird's life during its first calendar year (CY1) is from about June through December (see Figure 1). Each month we made close-range observations of up to 50 CY1, 50 CY2, 30 CY3, 20 CY4, and 50 definitive-plumaged ("adult") individuals and kept track of molt and change in appearance of all age classes. From January to July 1997 we simply observed birds in an attempt to understand molt and changing appearance, then from August 1997 to May 1999 we noted molt critically on 326 CY1, 429 CY2, 331 CY3, 146 CY4, and 350

	J	F	M	A	M	J	J	A	S	O	N	D
CY1: PA1					E	H		F	AAAAAAAAA..			
CY2: PA1	..AAAAAAA.. ? ?											
PB2	BBBBBBBBBBBBBBBBB											
PA2									AAAAAAAAA..			
CY3: PA2	..AAAAAAA.. ? ?											
PB3	BBBBBBBBBBBBBBBBB											
PA3									AAAAAAAAA..			
CY4: PA3	..AAAA.. ? ?											
PB4	BBBBBBBBBBBBBBBBB											
PA4									AAAAAAA..			
CY5+: PA4+	..AAAA.. ?											
PB5+	BBBBBBBBBBBBBBBBBBB											
PA5+									AAAAAA..			

Figure 1. Schedule of partial prealternate (A) and complete prebasic (B) molts of the Western Gull in central California. Mean egg-laying (E), hatching (H), and fledging (F) dates at Southeast Farallon Island are indicated for reference (Spear et al. 1986, Penniman et al. 1990). CY1, first calendar year; CY5+, fifth and subsequent calendar years, etc.; PA1, PB5+, etc., first prealternate, fifth and subsequent prebasic molts, etc. See Table 1 for ranges of starting and ending periods for each molt. Note that molts in CY1 and CY2 birds are only about two months earlier than in CY5+ and that with age prealternate molts appear to become shorter.

"adult" birds. We categorize our observations temporally as early (1–10th), mid (11–20th), or late (21st to end) in the month. Documentary photographs were taken of representative birds of each age class throughout the year. No birds were captured or individually marked.

We supplemented our sample from these two sites with opportunistic observations of birds from other areas in coastal California, from Sonoma to Monterey counties. Howell made incidental observations of *L. o. wymani* (approximately 100 CY1, 150 CY2, 80 CY3, 20 CY4, and 100 "adults") in May, August, and September 1997 and in February and November 1998 in Baja California, Mexico. In *wymani* molt may average slightly earlier than in *occidentalis*, although there is much overlap. We also examined freshly dead corpses for signs of active molt, as well as specimens at the California Academy of Sciences, to cross-check our field observations.

Given the wide range of variation in hybrid Western × Glaucous-winged (*L. glaucescens*) Gulls (Bell 1996), some of which are virtually indistinguishable from pure Western Gulls, it may be impossible to be certain of the purity of our sample. We restricted our observations, however, to birds that showed all characters of pure Western Gulls and, in summer, during the main period of prebasic molt, Glaucous-winged Gulls and their hybrids are rare in central California (pers. obs.).

In terms of anatomy, we use "mantle" to refer to the interscapular area only and "subscapulars" to refer to the four longest scapulars, i.e., those that

appear most posterior on a standing bird and are tipped boldly with white on adults and older immatures. Primaries (P) are numbered distally, i.e., the innermost primary is P1, the outermost P10. References to secondaries do not include the tertials, and greater, median, and lesser coverts refer to secondary coverts only.

RESULTS

Our study revealed that molt in immature Western Gulls is an almost continual process and that drawing lines on such a continuum is problematic. At first we attempted to fit our observations into the conventional framework of molt sequences, with a progression from juvenal to first basic to first alternate to second basic plumages, etc., with the second prebasic molt involving the first replacement of flight feathers (e.g., McCaskie 1983, Grant 1986). We soon encountered an inherent problem with this approach, however, and consequently we simply recorded the sequence and extent of molt as it happened, then attempted to interpret our observations. We found it most convenient to view molts as partial or complete, and here we describe the molt cycles of birds over their first four years of life.

Considerable individual variation, combined with potential overlap of successive molts, made it difficult to fit all birds into clearly defined categories. For example, the last stages of the first partial molt in April appeared to overlap with the start of the first complete molt, while the second partial molt appeared to start before the first complete molt had finished. Generally, partial molts appeared to occur largely within the span of scapular molt (which may not always be complete, however), while complete molts occurred largely within the span of primary molt.

Molt Cycles and Timing

Calendar year 1. Juveniles fledged (e.g., from Southeast Farallon Island) mostly during August (Spear et al. 1986), when they appeared commonly on the mainland coast of central California, with the first few birds in late July. The first signs of molt out of juvenal plumage were in late August (but mainly from mid September onward), with the appearance of new mantle and scapular feathers that often had very broad pale buff to pale cinnamon tips, giving some birds pale, almost leucistic-looking patches in their back; the pale tips soon wore off to reveal mostly gray-brown feathers. The subscapulars often appeared contrastingly fresh relative to the rest of the juvenal plumage and, together with the longest primaries, appeared to be the last juvenal feathers to become fully grown. Molt out of juvenal plumage then progressed through the mantle and scapulars as well as the head, neck, chest, and flanks. By late October, 75% of 91 birds had molted 50–60% (range 0–80%) of the visible scapular area, together with much of the head, foreneck, chest, and flanks. Molt continued through November and into December, by which time 80% of 57 birds had replaced 70–80% (range 10–90%) of their visible scapular area, most to all of the mantle, and much of the head, neck, chest, and flanks. The longest, underlying scapulars, including the subscapulars, were still juvenal plumage, as was the belly and often the

hindneck. There was no molt of upperwing coverts (nor, apparently, of underwing coverts), tail coverts (nor, apparently, of the rump), or flight feathers (including tertials) up to the end of CY1.

Calendar year 2. Molt continued slowly through the same areas from January to April or May, with juvenal feathers continuing to be replaced. Some of the mantle feathers replaced earliest had faded and appeared pale gray, suggesting the appearance of new feathers, but close-range views and examination of dead birds showed these feathers to be very abraded. Conversely, a few fresh gray feathers appeared on the mantles of some birds from late January onward. Molt continued through the scapulars into April and May, and some birds replaced most of their remaining juvenal scapulars during this period. The last scapulars to be replaced were generally the largest, underlying feathers and the subscapulars. These late-grown scapulars were often relatively dark, grayish or mostly gray, and fairly uniform, in contrast to the browner, faded, and more strongly patterned scapulars acquired months earlier.

The first bird we saw with a new subscapular was in early March, but not until April and May did many birds have one or more new fully grown subscapulars. The replacement of subscapulars in April and May corresponded with the completion of replacement of most or all juvenal scapular, mantle, head, neck, chest, and flank feathers. Birds at this time still had the belly mostly or entirely juvenal, and some showed scattered juvenal feathers elsewhere, especially on the hindneck. On some birds, however, the longest scapulars and subscapulars were not replaced until June or later.

The first complete molt started in early April when we noted the first bird with shed inner primaries, although not until late April and May did the majority of birds commence primary molt. By mid May, 78% of 37 birds had shed P2 or 3 (range 0–4), and by late May all birds had shed inner primaries. Also in April, birds started to drop median upperwing coverts and tertial coverts. In May and June, molt progressed quite rapidly and extensively, with most to all of the median upperwing coverts, most greater and many lesser upperwing coverts, some tertials, and many of the mantle and scapular feathers being renewed by late June; also by late June, most to all of the juvenal belly had been replaced. Most birds showed some to many new feathers in the chest, neck, and head, while one or two very "retarded" birds still retained a few very worn juvenal feathers in the neck. By mid June, 60% of 20 birds had shed P6 or 7 (range P5–8), with P1–4 new and P5 or 6 growing; no molt of tail or secondaries was noted through June.

Molt of rectrices started in early July: anywhere from the central pair to all but the outermost pair were shed almost synchronously, though with an overall inner to outer sequence, and a few birds appeared to have dropped the whole tail at once. Growth of rectrices was fairly rapid, and by mid to late August most birds had new apparently full-grown tails.

Molt of the secondaries started with the outermost feather in early to mid July, typically just after the initiation of rectrix molt, and continued inward, at times with groups of feathers shed almost simultaneously. By late August, a few birds had completed growth of new secondaries, but most completed this in September. The outermost primaries grew in fully between early

September and late October (mainly from late September to mid October). Thus the first complete molt extended from April to October, preceded by a protracted partial molt from late August through April or May (Figure 1).

Before the complete molt was finished, about 30% of 40 birds in mid to late August had shed and were growing new median upperwing coverts (i.e., replacing the feathers previously molted from April to June). The percentage of birds with replaced or newly growing median coverts increased to 67% (n = 21) by late October, although we detected with certainty no molt in other tracts by this period. The new incoming median coverts varied from patterned brownish (much like the surrounding upperwing coverts) in early molting birds to unmarked gray (in strong contrast to the other upperwing coverts) in late molting birds. By late November at least 80% of birds (n = 23) had replaced median coverts and molt of these feathers appeared to have ended. The ratio of birds with new brown to new gray median coverts was about 50:50, and the replaced feathers ranged from a group of a few to most of the inner or outer coverts, with no apparent pattern of replacement. Few if any birds replaced all of their median coverts. In November we also noted birds with scattered new gray lesser upperwing coverts, as well as new feathers in the face and, apparently, the mantle and shorter scapulars; one bird also had replaced two inner greater upperwing coverts and its tertials with new grey feathers. This partial molt continued slowly through December in the head, mantle, and scapulars.

Calendar year 3. Molt continued at variable rates in the scapulars, mantle, head, neck, chest, and sides through April and probably into May, by which time all birds appeared to have replaced most feathers in these areas. Usually, a few old scapulars were retained, and we saw no subscapulars replaced in this molt. We also detected no molt of belly, rump, tail coverts, or wing coverts during this period. Thus, the extent of this protracted partial molt was similar to that in the previous year, but often this molt also included some median and lesser upperwing coverts. Interestingly, the incoming plumage typically comprised variably dusky clouding on the head, neck, and chest, so the white-headed "second summer" plumage came about largely through wear and bleaching of these feathers.

Inner primaries started to be shed from late April through late May, along with median upperwing coverts and tertial coverts, signaling the start of the second complete molt. Molt continued through the summer, much like that in the previous year, although averaging slightly later. For example, by mid May, 76% of 34 birds had shed P2 or 3 (range 1–4), and by mid June, 75% of 20 birds had shed P5 or 6 (range P3–7), with P1–3 new and P4 or 5 growing. Tail molt started from early to late July, and by early to mid September almost all birds had fully grown new tails. Secondary molt started in mid to late July and largely ended in mid or late September. The belly was mostly replaced by mid June, although a few birds retained brownish belly feathers into early July. Traces of new dusky markings on the head and neck first appeared in mid June (about when P7 was shed). This second complete molt finished with full growth of outermost primaries between early October and early November.

The first bird noted with renewed molt of median coverts was in late

August; by mid September 20% of 24 birds had growing or newly replaced median coverts, increasing to about 50% of 21 birds by mid to late October. Through November we detected no molt in other tracts, but detecting any change, e.g., from gray to gray in the scapulars or wing coverts, would have been difficult.

Calendar year 4. From the previous December through at least February or March, the mantle, scapulars, head, and neck underwent a molt much like that in CY3. Molt was harder to detect than in younger age classes because of the greater similarity of old and new feathers and the old feathers' being less worn, relatively, because of a shorter period between molts. Therefore we were unable to distinguish at what point the third partial molt ended. A few birds also replaced one or two inner greater coverts and up to four or five additional median coverts during December and January.

The third complete molt (into definitive plumage) started with the dropping of inner primaries and median upperwing coverts from mid May to mid June and continued in apparently the same sequence as did the complete molts during CY2 and CY3, although averaging later in the year. For example, by mid May 55% of 18 birds had not started primary molt (range P0–2 shed), and by mid June molt of primaries in six birds had reached only P2–4 shed, with P1–2 new and/or growing. Tail molt and secondary molt started from late July to mid August. The first traces of new dusky markings on the head and neck appeared in late July (about when P7–8 were shed).

This third complete molt appeared to finish with full growth of the outermost primaries between mid October and early to mid November; however, once the tail had been shed, distinguishing CY4 birds from adults became problematic, and accurate determination of the timing of completion of molt in this age class should await study of birds of known age.

Gray scalloping acquired on the head from late July through September was often so fine that it was hard to see; presumably it could wear off quickly, leaving the head and neck white. Thus determining the timing and extent of any partial winter–spring molt of the head and underparts on birds in definitive plumage is almost impossible without in-hand examination.

The first birds with dropped median coverts were noted in late September, and three birds in mid October showed active median-covert molt. After this time, we could not age birds confidently to determine subsequent molt in this age class.

Calendar year 5 and after. The percentage of cleanly white-headed "adult" birds increased from around 50% in early January (n = 50) to 95% by early March (n = 50), although we could not ascertain how much molt, as opposed to wear, was responsible for this change. At least some scapulars were molted over the winter, from January (and probably December) through February or later, and a few birds also replaced some inner greater and median upperwing coverts during this period, i.e., much like those in CY4.

The complete molt of adult-plumaged birds started between mid May and early July, this span presumably reflecting variation in the birds' age and breeding status. Limited data on known breeding adults (from SE Farallon Island and Bodega) indicated that primary molt of breeders started between

early June and early July (i.e., after eggs had hatched). Larger samples may reveal some breeders starting primary molt even earlier, as has been found in the Herring, Lesser Black-backed (*L. fuscus*) (Ginn and Melville 1983), and Glaucous-winged Gulls (Verbeek 1993).

This definitive prebasic molt started with the shedding of median upperwing coverts, tertial coverts, and inner primaries and apparently progressed much as in other age classes, although distinguishing generations of white head and body feathers generally was not possible. In mid May, 82% of 27 birds had not yet dropped primaries (range 0–2 shed), and by mid June, 90% of 20 birds had shed P1–3 (range 0–3). Tail molt and secondary molt started from mid August to late September. Faint dusky markings appeared on the heads and necks of some birds in mid or late August (about when P7–8 were shed), while others at the same molt stage had apparently fresh, almost glossy white head feathers, with no trace of dusky markings. In September, up to 75% of 50 birds showed dusky markings on their head and neck, and in October at least 90% of 50 birds had such markings, which varied from light scaling (hard to see except at close range) to moderately heavy dusky mottling and streaking. This complete molt finished with full growth of outermost primaries between early November and late December, although most birds had fully grown outer primaries by early December.

The first adults with dropped median coverts were noted in early October, and birds with active median-covert molt were noted through December. We were unable to detect molt in other tracts because the change would be largely from gray to gray and from white to white feathers, almost all of which were relatively fresh at this time. Whitening of the heads appeared largely due to wear through December, and by January up to 50% of adult-plumaged birds appeared white headed (see above).

Molt Sequence

While field observations allow molt to be followed in large numbers of birds, they do not allow critical data to be taken for all areas of a bird. For example, we were unable to determine the exact timing and extent of molt of the rump or underwing coverts, areas generally hidden when birds are perched; in addition, molt of tail coverts was often difficult to ascertain. Nonetheless, some general observations can be made on the sequence of feather molt in the Western Gull, and this same overall sequence appears broadly similar in several other species of large gulls (pers. obs.; Howell et al. 1999). Judicious collecting of specimens or recapture of known individuals could help refine our review of molt sequence.

Typically, the first partial molt started with the shorter scapulars and mantle feathers, followed by the sides of the chest and the lores, and proceeded through the head, neck, chest, and flanks. The last feathers to be molted were usually those of the hindneck and the longest scapulars. No wing coverts, tail coverts, flight feathers, or, apparently, belly and rump feathers were replaced. Subsequent partial molts often started with the median upperwing coverts (often dropped almost simultaneously, or with the outermost feathers dropped first), followed by the scapulars and mantle

feathers, and ended with the head and longest scapulars. In second and subsequent partial molts, some upperwing coverts (especially the median coverts) were often, but not invariably, replaced, and some scapulars also may not always be replaced. The subscapulars appeared to be replaced in partial molts only by some birds in CY2, but their growth and replacement was protracted and often appeared asynchronous, so it is possible that some individuals of older age classes replace one or more subscapulars during partial molts.

Complete molts started with the median upperwing coverts, inner greater upperwing coverts (especially the tertial coverts), and inner primaries. Body feathers followed (including the belly, fairly early on) as lesser and greater upperwing coverts and tertials were replaced. Often the median coverts were dropped almost simultaneously, along with some tertial coverts, followed by the outer greater coverts and the row of large lesser coverts immediately above the median coverts. The greater coverts continued to be replaced inward while the remaining lesser coverts were molted. Rectrices started to drop when primary molt reached about P7 being shed, and secondary molt started at the same time or shortly thereafter, from the outermost secondary inward. Complete molts ended with the inner secondaries, adjacent to the tertials, some subscapulars, and finally the full growth of the outer two primaries.

DISCUSSION

Timing and Extent of Molt

The conventional view proposed by Dwight (1925) for the Western Gull and repeated with no modification by Pierotti and Annett (1995) is of a partial first prebasic molt from September to November, a partial first prealternate molt during March and April, and subsequent prebasic molts in August and September, followed by partial prealternate molts during March and April. McCaskie (1983) recognized that these molts were more protracted and gave their spans as July to October and February to April.

The molt periods are not as neatly defined as those authors suggested, however, and molt appears to be more or less continuous for at least the first two years of a Western Gull's life. Our observations suggest that approximate molt cycles can be superimposed upon this continuum (Table 1, Figure 1). The first and second partial molts span up to 7 or 8 months, while subsequent partial molts appear to be shorter in duration and perhaps less extensive. Younger birds, which are not breeding, can undergo more prolonged and more extensive partial molts than breeding adults, which have only a short period between finishing their complete molt and starting breeding. The feather quality of first-year birds also may be poorer than that of adults, resulting in the need for a more extensive first partial molt. Complete molts for all ages take 5 or 6 months, as has been reported for the Herring Gull (Pierotti and Good 1994).

The first partial molt generally involves the head, neck, chest, flanks, mantle, and scapulars, while in later molts these feathers and often some median and lesser upperwing coverts are replaced. Trapping live birds, or

Table 1 Approximate Periods of Partial Prealternate (PA) and Complete Prebasic (PB) Molts of the Western Gull in Central California

Molt	Starting period	Ending period
PA1	late Aug–late Oct	Apr–?[a]
PB2	early Apr–late May	early Sep–late Oct
PA2	mid Aug–mid Nov	Apr–?
PB3	late Apr–late May	early Oct–early Nov
PA3	late Aug–?	Mar–?
PB4	mid May–mid Jun	mid Oct–mid Nov
PA4	late Sep–?	Feb–?
PB5+	mid May–early Jul	early Nov–late Dec
PA5+	early Oct–?	Feb–?

[a]See text for problems in determining periods of prealternate molt.

targeted collecting of specimens, could help determine the full extent of partial molts, e.g., whether or not any rump or belly feathers are replaced. Variability in the availability of food and the experience and fitness of foraging birds may mean that not all feathers within a tract are always replaced in a given molt. For example, while all scapulars and median coverts are replaced in every complete molt, they are not necessarily replaced in every partial molt.

The longest scapulars, because of their size, may be the most energetically costly feathers to replace in a partial molt. Because the juvenal subscapulars are replaced for the first time between March and June, or later, it is not possible to determine at what point the first partial molt ends and the first complete molt begins—unless one can know the history of every scapular follicle and how many times it has been activated. That is, by the end of the first complete molt, some scapulars (the shorter feathers) may have been replaced twice, while others (the longer feathers and subscapulars) have been replaced only once.

Molt of the median upperwing coverts may parallel that of the scapulars; i.e., if median coverts replaced in April are not replaced again in the fall through winter, then their replacement in April would pertain to the first complete molt, but if they *were* molted again in fall then their replacement in April might pertain either to the end of the first partial molt *or* to the start of the first complete molt. Because all Western Gulls of all ages replace all of their median coverts from April to June, concurrent with the shedding of inner primaries, we consider (for the purposes of molt terminology) that replacement of median coverts at this time is part of the complete prebasic molt.

Molt Nomenclature

Humphrey and Parkes (1959) proposed a nomenclature (the so-called H–P system) that facilitates an objective study of molt and plumage homologies among all groups of birds, and the H–P system is standard for molt studies

in North American literature. By the H–P definition, the complete molt in adults of all species, usually after breeding, is considered a homologous prebasic molt. Similarly, the first molt that succeeds juvenal plumage has always been considered the first prebasic molt. Following traditional use of H–P terminology, the protracted "postjuvenal" molt of a Western Gull would be a partial first prebasic molt. If, however, one traces the partial–complete–partial–complete molt cycles in a Western Gull back from the complete, definitive prebasic molt to juvenal plumage (Figure 1), the homology of the first partial molt lies with a *prealternate* molt. That is, the first partial molt is similar in timing, duration, and extent to the second prealternate molt, which argues strongly in favor of treating the first partial molt as a prealternate molt. Consequently, there is no partial first prebasic molt in a Western Gull's first year; the molts of first-year Western Gulls are only two to three months ahead of those of adults, and the molting periods converge over three years of predefinitive plumages (Figure 1). The main difference between the first and subsequent partial molts is that the latter often include upperwing coverts. California Gulls (*L. californicus*), however, which have a similar molt strategy to Western Gulls', can replace upperwing coverts in their first partial molt (see below).

That the homology of the first partial molt with a prealternate molt in the Western Gull has been widely overlooked may be attributed to the protractedness of the first partial molt, the continually changing appearance of plumages, and, perhaps, the tradition that fall molts are prebasic, spring molts prealternate. For example, Parkes (1967) noted "we have encountered, thus far, no bird species with two definitive ("adult") plumages per cycle which does not also have two corresponding plumages in its first year." Unless populations were followed over time, however, it would be easy to examine late winter specimens of Western Gulls and assume that any molt was a second molt.

That the same feathers of the same generation may look different on different individuals, depending on the time of year they are replaced, is not widely appreciated, although this phenomenon was demonstrated conclusively for the White Ibis (*Eudocimus albus*) by Kushlan and Bildstein (1992) and has been mentioned for some passerines such as tanagers (Pyle 1997). It could be argued that new gray feathers appearing on the mantle of Western Gulls from late January onwards signify a new molt, and indeed this would be difficult to disprove without detailed study over time of known individual birds. Ongoing observations of the entire molting process, however, lead us to infer that retained juvenal feathers were being replaced by feathers different in appearance (more "advanced") than those grown in during early winter. This hypothesis is supported by observations of molt in the scapulars, in which individual feathers are easier to distinguish than on the mantle. It was clear that scapulars replaced later were often relatively plain and dark grayish, in striking contrast to the strongly patterned brownish scapulars acquired earlier. Regardless of whether these late-molted scapulars pertain to the preceding partial molt or succeeding complete molt, there are at most only two postjuvenile generations of scapulars in a bird's first year, not up to three as would be required for a scenario of partial prebasic, partial prealternate, and complete prebasic molts within this

period. That the first partial molt is almost identical in timing and extent to the second partial molt (Figure 1) also argues against any second partial molt of some feathers late in the first winter, because this has no equivalent in later plumage cycles.

Our reinterpretation is supported by, and also helps explain, the results of Howell et al. (1999), who described the traditional "first prebasic molt" of migrant Herring, Thayer's, and Glaucous-winged gulls wintering in central California. Those authors noted that the juvenal plumage of these species was often retained into midwinter, and that some juvenile Thayer's Gulls in March had not started to molt. Ironically, they asked "do first-year large gulls even have a prealternate molt?" because, given conventional understanding, the first prebasic, first prealternate, and complete second prebasic molts would have to occur after birds left California in April and before they returned in November. Our studies of the Western Gull help solve this problem if, instead, there are simply one partial (prealternate) and one complete (prebasic) molt in this period.

We are aware of two other studies, based on critical observation and examination of specimens, that reached similar conclusions regarding the first-year molt of certain species. For the California Gull, Johnston (1956) noted that the traditional division into first winter (prebasic) and first nuptial (prealternate) molts and plumages was misleading. He concluded that "It would be appear to be more accurate to speak of a first winter molt, involving, for the most part, only the feathers of the upper back [i.e., mantle and scapulars] until February when a rather extensive molt of the body, head, and neck areas commences." Thus, by spring, as in Western Gulls, no feather tracts of California Gulls have been replaced more than once, and subsequent molts follow the cycle of complete prebasic and partial prealternate. Johnston's study predated the advent of H–P terminology, and his conclusions have been overlooked.

We note, though, that "postjuvenile" molt in early fledged California Gulls in central California in fall 1998 tended to be more extensive than described by Johnston (1956), often involving much of the head, neck, chest, and flanks, as on Western Gulls (pers. obs.). On some birds (typically those with the most extensive scapular molt) this molt also included some inner median and greater upperwing coverts. We detected no second molt in spring of any CY2 California Gulls, however, and the changes in appearance of birds in late winter and spring were due largely to feather wear and bleaching.

Kushlan and Bildstein (1992) undertook a careful study of the White Ibis and concluded "the existence of an alternate I plumage is not documented." We suggest the molt strategy of the White Ibis is like that of large gulls, and instead it is a first prebasic molt that is lacking.

The problem of following individuals and populations over time, combined with the variability in feathers of the same generation, has hindered recognition of the molt strategy manifested by the Western and California gulls and the White Ibis. A provisional review suggests that this molt strategy is typical of most (if not all) large gulls and of several large wading birds, including the Black-crowned Night-Heron (*Nycticorax nycticorax*) (Howell, unpubl. data). We encourage a fresh look at molt in nonpasserines and more critical study of their strategies.

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