IN THE SCOPE

Molt and Plumage: A Primer

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Just over 50 years ago, Humphrey and Parkes (1959) published a paper in the *Auk*, the journal of the American Ornithologists’ Union, with far-reaching implications and effect. The paper’s title, “An approach to the study of molts and plumages,” may seem rather benign, but it described a systematic way to treat the subject that had heretofore been lacking. While the Humphrey-Parkes system (widely known as the “H-P system”) has not been universally accepted, it remains the sole system of naming molts and plumages that is internally consistent and requires no alterations, no matter what species of bird on the planet one considers.

This essay is the first of a multi-part effort to explain the respective strategies that various bird groups use to replace their plumage. (The other installments in the series will not follow in metronomic fashion.) This article is intended as a broad introduction to the topic, and subsequent essays will examine certain subjects in more detail.

If you do not understand parts of what follows, do not despair! The topic is quite complex, and anyone thinking that he or she understands everything the first time through is probably deceiving him- or herself. I know that I’m still learning aspects of the topic, and I’ve been working on it for, literally, decades. But with a little effort, anyone can gain a basic understanding of molt—and understanding molt can vastly improve a birder’s skills, as we shall see.
What

Molt is the act of replacing feathers in a systematic way. It can seem complex and confusing to us humans because birds have “co-opted” molt to fulfill many purposes in addition to the simple replacement of worn feathers. Molt has diverged into a plethora of strategies to fit the lifestyles and needs of the world’s birds, with individual species “designing” (through survival of the fittest, of course) their own molt strategy if and when the need arises.

The simplest definition of a molt is the replacement of a discrete set of feathers, either all of the feathers or some subset. Thus, a molt can be viewed as the transition between the previous set of feathers and the subsequent one. These sets of feathers created by molts are called plumages. Plumages can be made up either of entirely new feathers or a mix of old and new feathers.

Why

While bird feathers, gram for gram, are very strong, they need to be very light; thus, they wear out. Birds developed a way to deal with the problem so long ago that their dinosaurian forebears may actually have been the ones to develop it.

See Figure 1 on the back cover. The very ugly Herring Gull depicted there is as good an example as I’ve ever seen of the need for birds to replace their plumage. This individual, for whatever reason—probably poor health—has delayed one, or even two, of its molts. The picture was taken in June and, judging by the state of its primaries, which are worn and bleached, the bird probably did not replace them in its prebasic molt the previous fall. The wing coverts, which are also extremely worn, had two chances to be replaced: once in the previous fall’s prebasic molt and again in the spring’s prealternate molt.

When

In most bird species, molt is conducted on an annual basis in order to maintain the plumage and fitness of individuals. The simplest strategy is to replace feathers once per year, and probably more species use this strategy than any other. However, even the annual strategy has seen schism—most such species molt all their feathers once per year, but others replace only a subset of feathers each year (meaning that some feathers are more than one year old). These species are primarily large ones for which the time and energy required to replace all feathers, particularly the large flight feathers of the wings, are prohibitive. This “large-bird” strategy will be discussed in its own essay in the future.
Through time, as birds have used molt for adaptive reasons other than strict feather-coat maintenance, molt strategies have multiplied. Now, many species conduct two molts annually, with some adding a third. As molting is an energy-expensive process, birds generally constrain molts to periods when they are not performing other energy-expensive processes like breeding or migration. Though many bird species conduct multiple molts in a year, virtually all species conduct a molt after breeding, whether or not it is their only molt of an annual cycle.

Where

Most individuals of most bird species conduct a molt on or near the breeding grounds immediately or shortly after the breeding season. This is because for most species, the time immediately after breeding is one of few, if any, parental responsibilities and of relatively high resource availability.

As with most aspects of biology, there are many exceptions to this “rule.” If the above can be thought of as molting-location strategy #1, then the other such strategies are:

2. molt on the wintering grounds;
3. initiate molt on the breeding grounds, suspend it, and then complete it on the wintering grounds;
4. molt in some third area, which is sometimes (but not always) in between the breeding and wintering grounds.

There are varieties of each of the above strategies that might best be termed tactics, but most species utilize one of these four general approaches. Other strategies may exist, but most of the world’s bird species have been very little studied when it comes to molt.

Modified Humphrey and Parkes (H-P) terminology

Humphrey and Parkes (1959) proposed a solution to the problem of identifying plumages, and the molts that produce them, without the confounding aspects of calendar or location. Though the terms remain well-used, “winter plumage” and “breeding plumage” are difficult to define because there are so many exceptions. Good examples of the problems inherent in this “system” are legion, but I present a couple as example of the need for more rigorous nomenclature:

1. Many bird species that breed at high northern latitudes and which spend the non-breeding season south of the equator are in “winter plumage” in the Southern Hemisphere’s summer and mix with other species, resident and migrant, that are in their “summer plumage” in the Northern Hemisphere’s winter.

2. Many duck species conduct courtship and pairing behaviors in
winter, thus such species are in “breeding plumage” in winter. In fact, the only time that males are not in “breeding plumage” is in summer and early fall, and females breed in “non-breeding” plumage!

See Figure 2 on the back cover. This pair of Gadwall was photographed in mid-March, but the male has been in this “breeding plumage” since, at least, the previous October, and he will retain it until May or June, at which point he will molt into what has been termed “eclipse plumage.” The female has initiated her molt into “eclipse plumage” and will retain that plumage until fall. The very different molt tactics of ducks will be more thoroughly treated in a subsequent essay.

The Humphrey and Parkes (hereafter, the “H-P system”) terminology separates aspects of molt and plumage from other considerations and identifies molts based on their homology (that is, shared ancestral history) across species. Howell et al. (2003, 2004) modified one of the basic tenets of H-P in order to allow the system to account for discrepancies first articulated well in studies of gull molt (Howell et al. 1999). I summarize the modified system below.

The basis of the modified system is that the “first coat of pennaceous feathers” (Pyle 2008), which is often called “juvenal plumage,” has now been defined as “first basic plumage” (Howell et al. 2003). From this point, all subsequent plumages are derived via discrete molts with consistent nomenclature: prealternate molts (abbreviated PA) produce alternate plumages (A), while prebasic molts (PB) produce basic plumages (B).

**One molt per year**

Plumage cycles are defined on the basis of prebasic molts: a plumage cycle is the time between the initiation of one PB molt and the initiation of the next one. In species in which only one molt is conducted per year, there is only one plumage—basic—no matter how the bird’s appearance (or “aspect”) may change through the year. European Starling is one such species; its appearance changes from winter to summer due to feather wear, not replacement of feathers.

In slow-developing species, individual PB molts may differ in their extent or timing and/or provide for varying appearances (aspect), as in eagles. In such species, molts and plumages can be numbered until adult or definitive aspect is reached. Thus, one can differentiate juvenile Bald Eagles (in juvenal or first basic plumage, or B1) from one-year-olds (B2), from two-year-olds (B3), and from three-year-olds (B4). Once plumage aspect has stabilized in the adult or definitive appearance, one can no longer discern the precise age of the bird, so this plumage is termed definitive basic (DB) plumage. In
Bald Eagles, definitive basic plumage is characterized by a clean white head and tail, among other features.

See Figures 3 and 4 on the back cover. The Northern Mockingbird in Figure 3 is in juvenal or first basic plumage (B1). The species is a good example of one with a simple molt strategy, conducting only one molt per year (but see below). The Bald Eagle depicted in Figure 4 is in second basic (B2) plumage, having conducted one molt—the second prebasic (PB2)—since leaving the nest, and is probably a bit under two years old.

**Multiple molts per year**

Species with more than one molt per year are considered to have inserted an extra molt (or two) into the cycle between pre-basic molts. Extra molts have been inserted in many species that inhabit harsh environments or are exposed to more sun annually, meaning they need to replace worn feathers more often than once per year. Extra molts can also occur in colorful species, long-distance migrants, and species with strong sexual selection of male appearance, but there are species exhibiting all three of these traits that conduct only one molt per year (e.g., longspurs and Red-winged Blackbird).

The most common inserted molt is the prealternate (PA) molt. Again, in slow-developing species that have them, such as gulls, PA molts can be numbered until the individual achieves adult plumage: the first prealternate molt (PA1) produces first alternate plumage (A1), the second prealternate molt (PA2) produces second alternate plumage (PA2), et cetera.

In many species, prealternate molts serve to increase “attractive-ness” for the purposes of holding territories and/or mating (although there are many species, including flycatchers and wrens, that do not change appearance markedly in the prealternate molt). In species that do change appearance, the prealternate molt is often limited to the head and the chest and/or particular badge features (e.g., the head patterns of *Zonotrichia* sparrows). In slow-developing species, such as gulls, the earlier prealternate molts seem to be a way to advance plumage maturation, but the reasons are unknown, as most such birds do not breed in these plumages (e.g., A3 California Gulls).

Whereas prealternate molts occur in most or all cycles, another inserted molt occurs only in the first plumage cycle: the preformative molt, which produces formative plumage. Thus, formative plumage is unlike alternate plumage, which is inserted into every year of a bird’s adult life. This difference explains my contention that alternate plumages are more common even though formative plumages are more widespread. Yes, more species exhibit formative plumages
than exhibit alternate plumages—and some species sport both—but a particularly long-lived Herring Gull, for example, will exhibit only one formative plumage in its life, whereas it will exhibit alternate plumages in each of its 35 years of life.

The aforementioned Northern Mockingbird (Fig. 3, back cover) provides a good example of the ephemeral nature of first basic (or “juvenal”) plumage in many passerines. This juvenile probably began replacing parts of its first basic plumage with formative plumage only a couple weeks after leaving the nest, at less than a month old. Those who do not bird in mid-summer will only rarely encounter birds in first basic plumage, though many larger species have less ephemeral first basic plumage. Because it disappears so quickly in many species, this plumage provides one of the easiest and surest methods to “confirm” a species as breeding locally (but beware the species that do migrate in this plumage!).

The final inserted molt is a presupplemental molt, which produces, of course, a supplemental plumage. Presupplemental molts are generally inserted only into definitive plumage cycles (that is, they occur only in “adult” birds), but there are some exceptions. Although a few common species exhibit this molt (e.g., terns and some Passerina buntings), it is poorly studied and little understood. These molts are variable in timing by species and, in some species, by age and/or sex! In some species, they may precede the prealternate molt, in others succeed it (Pyle 2007). As an example of how extreme some species may be, some Least Terns have been shown to replace some inner primaries as many as three times (that is, go through four generations of those feathers) in their first plumage cycle (Pyle 2008, figure caption on p. 17).

For now, it is enough to know that presupplemental molts exist. Should these molt essays continue to the point at which I am discussing presupplemental molts in detail, it will mean both that I have written a lot of these essays and that I will have learned an awful lot more about presupplemental molts than I currently know!

Molt strategies

As the final aspect of molts and plumages presented here, Howell et al. (2003) introduced the concept of molting strategies (not to be confused with the molting-location strategies noted above!), defining four such strategies as follows:

Simple Basic Strategy (SBS): No inserted molts in the first or definitive cycles (Fig. 5A).

Complex Basic Strategy (CBS): One inserted molt in the first cycle and no inserted molts in definitive cycles (Fig. 5B).
Simple Alternate Strategy (SAS): One inserted molt in the first cycle and one inserted (prealternate) molt in definitive cycles (Fig. 5C–E).

Complex Alternate Strategy (CAS): Two (rarely three) inserted molts in the first cycle and one (occasionally two) inserted molt in definitive cycles (Fig. 5F–H).

Figure 5 is a reproduction of Pyle’s (2008) Figure 10. I strongly recommend obtaining your own copy of Pyle’s book. On the back cover, I have provided species examples of SBS (Bald Eagle), CBS (Northern Mockingbird), and SAS (Gadwall and Herring Gull).

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Figure 5 (from Pyle 2008, used with permission). Examples of timing and extent of molts in North American birds. A: Simple Basic Strategy (SBS). B: Complex Basic Strategy (CBS). C, D, E: Simple Alternate Strategy (SAS), three examples differentiated by the timing and extent of the second molt. F, G, H: Complex Alternate Strategy (CAS), three examples differentiated by the order and number of inserted molts. See text for molt abbreviations.
LITERATURE CITED

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In the Scope: Molt and Plumage . . . 135

Fig. 1. Herring Gull, Prime Hook National Wildlife Refuge, Sussex County, DE, 11 June 2008.

Fig. 2. Male and female Gadwall, Sands Lake, Chaffee County, CO, 14 March 2007.

Fig. 3. Northern Mockingbird, Villas, Cape May County, NJ, 13 July 2009.

Fig. 4. Bald Eagle, Cherry Creek State Park, Arapahoe County, CO, 12 February 2005.
All photos by Tony Leukering