A BASIC UNDERSTANDING OF MOULT:

WHAT, WHY, WHEN, AND HOW MUCH?

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Various papers have been written about moult. Those that most people remember compare basic and alternate plumages (the Humphrey-Parkes system) to winter and summer plumages (the traditional system), and try to help people make the transition between the two terminologies. These are good articles and have been very helpful. Nonetheless, I still encounter a widespread misunderstanding, almost a fear, of moult among many birders, even experts. Derived largely from conversations with these birders, this note is an attempt to explain the what, why, and when of moult, and to provide a conceptual grounding by showing how moult fits into a bird's life cycle. Armed with this understanding, looking at moult characteristics can be useful for field identification at the levels of species, population, and age/sex (e.g., see Pyle 1997), and can make better birders out of us all.

Ground Zero

We must recognize at the start that moult is a dynamic, evolutionary process, just like speciation. Over the enormity of time, selection has favoured the moult strategies we see today; we can only guess at the routes taken, and we should realize that moult strategies evolve in response to changing environmental parameters.

As is often the case, nature is too complex to be pigeonholed, and in the same way that ornithologists argue over the merits of different species concepts, there are arguments over the merits of different systems for studying moult. Many "problems" may be of the kind that lie between the chair and the keyboard, others may be genuine exceptions that challenge us to explain them. Considerable recent progress has been made in the study of moult following the far-sighted work of Humphrey and Parkes (1959, 1963), and it is widely accepted that the Humphrey-Parkes system is the most helpful framework for studying moults and plumages. Anyone with a serious interest in moult should read and assimilate these seminal papers.

What is Moult? And Why?

Moult is "simply" the replacement of feathers. It is also one of the most fundamental processes of any bird's life cycle: every bird on Earth needs to moult, whether adult or immature, breeding or non-breeding, migratory or resident, penguin or hummingbird. Feathers are not permanent structures – they wear out from simple day to day exposure to a variety of elements such as sun, rain, and abrasion, and need to be replaced. Although they grow from follicles in the skin, much as our hair does, new feathers push out old feathers, and distinct seasonal plumages comprise distinct coats of feathers. Thus, moult in birds is a cyclic process rather than a continuous renewal process like human hair.

When to Moult?

This is where things become a little more complicated. To understand the when of moult it may be best to step back and imagine an evolutionary scenario. You should also consider that feather replacement requires energy, and so far nobody has documented gratuitous moult: birds moult for a reason.

Let's say a bird evolves, the ancestral bird in a primordial and essentially aseasonal environment. Its plumage protects it from exposure and death, but feathers will wear out and need to be replaced. In order to grow new feathers the bird needs enough food and energy, so feathers get replaced at times when, and/or in areas where, food supply is good. If food supply and exposure to the environment are more or less constant, moult may be essentially an ongoing process without strong seasonal peaks, at least within a species. In fact, some tropical birds in aseasonal climates still show year-round patterns of moulting. In particular, though, the replacement of larger feathers demands more energy and, over time, moult cycles may become honed to regimes of food supply which, in turn, are affected by variables such as climate. In areas with a seasonal climate and distinct peaks in food supply, moult may become concentrated to correspond with these peaks: for example, late summer flushes of seeds and insects in North America. Thus, moult cycles mirror a far larger picture.

Another fundamental, energy-demanding aspect of a bird's life cycle is breeding, so it should not be surprising that active moult is generally reduced or arrested altogether during this season. Then, after energy-demanding phases of breeding such as territory defense and copulation, or egg production and laying, have passed moult can start again. Although moult and breeding typically do not overlap, this depends on the species involved and on how one defines "breeding." In general, larger species take longer to replace their more numerous and larger feathers than do small species. Therefore, once the last eggs of a season are laid, larger birds, including many seabirds and waterfowl, often start moulting again. Smaller birds, on the other hand such as warblers, can wait until their young have fledged and still have time to replace all their feathers before migration or before winter sets in.

During the breeding season, feathers often become heavily abraded from entering and leaving nests, or from birds singing for long periods from exposed perches. Moulting in fall replaces these worn feathers and provides a coat of new feathers that can better protect and insulate a bird through potentially bad winter weather. Thus, moult occurs at the "perfect" time to balance these factors.

A second major energy demand that can conflict with moult is migration. As with breeding, birds typically don't moult during the energy-demanding phases of migration, and long-distance migrants exhibit various strategies to balance moult and migration. If there's enough food and time before migration, then adults moult before heading south, for example, Lesser Nighthawk, and most passerines, including Baltimore Oriole and eastern populations of Painted Bunting (Pyle 1997). If there's not enough time and/or food before migration, or perhaps if there's more food during migration or on the winter grounds, then birds migrate and then moult at migration stop-over sites and/or on the winter grounds, for example, Common Nighthawk and some passerines including Bullock's Oriole and western populations of Painted Bunting (Pyle 1997). In which hemisphere birds winter may also be important: long daylight hours in the southern hemisphere often mean more food, and thus better conditions for moulting, than the short days of the northern hemisphere fall and winter. In some cases, birds may suspend moult during migration; that is, they start to moult before migration, then stop moulting, migrate, and finish moult after migration (e.g., various shorebirds and terns). Furthermore, different populations or age-classes of a species may employ different moulting strategies, which can be of relevance to field identification. For example, all Hammond's Flycatchers moult in late summer before migrating, while adult Dusky Flycatchers typically migrate to their winter grounds in Mexico before moulting (Pyle 1997): thus, a heavily worn Dusky/Hammond's Flycatcher found on fall migration should be a Dusky.

Basic and Alternate Plumages

Using basic and alternate as terms for plumages is best done if you forget summer and winter, or breeding and non-breeding – imagine switching to driving on the other side of the road, but doing it only on Mondays, Wednesdays, and Saturdays! So, I'm not going to provide a "conversion table" here to equate basic plumage with winter plumage, or any of that. (Why? Because the two are often *not,* in fact, synonymous, and all that results is confusion!) Instead, I'll throw out an evolutionary thesis that may help in understanding what these plumages are. At the same time, while understanding the concept of basic and alternate plumages is critical to studying the evolution of moult and plumage sequences, using the terms "breeding" and "non-breeding" for many species' plumages still may be the most meaningful and useful system for many birders in the northern hemisphere. These two systems are different, but one is not necessarily better: which you use depends on your purpose.

Back to our ancestral bird. Let's say it replaces all of its feathers once over a cycle of time that, for the sake of argument, we'll call a year. This plumage it replaces once a year is called its basic plumage, because that's what it is – basic plumage, regardless of when it is attained. In this case, the bird simply moults from one basic plumage to another basic plumage to another, each year. By definition, the basic plumage is replaced completely, or nearly completely, once a cycle, and the moult by which it is attained is the prebasic moult. Although most birds in the world do this, most birders and ornithologists live in temperate northern climates, where such species are "exceptions." Consequently, we tend to have a warped view of the bigger picture. Think about a Northern Fulmar, or a Red-tailed Hawk – they have one moult a year; so does a pigeon, or a woodpecker, or a starling. What could be simpler? We're just stuck with so many gulls, shorebirds, and warblers that the basic facts have become obscured.

Some birds have feathers that wear out more quickly than others because, for example, these birds live in harsher environments, or fly long distances during migration. Thus, certain feathers may need to be replaced more than once a cycle – maybe the head feathers of a bird that lives in exposed environments, or the scapulars and upperwing coverts that protect the major wing feathers of birds that fly long distances. As with any moult, these extra moults become honed to food supply and fit into the bird's annual energy cycle, but in theory they could occur at any time of year. However, if hormones associated with the start of the breeding season affected feather pigmentation, and if these extra moults corresponded with the start of the breeding season, then a different-looking plumage might result. Perhaps this could be brighter, or "fancier" than the basic plumage, perhaps more cryptic and better suited to camouflage on the breeding grounds? Over time, forces such as sexual selection or predation may have enhanced and refined these random variations, these alternate plumages, and they have become a regular part of a bird's annual cycle; and alternate plumage is attained by a prealternate moult. Although we tend to associate alternate plumage with breeding plumage this is not a good idea – the terms alternate and basic were proposed to free studies of moult from such preconceptions. Thus, an alternate plumage is any second plumage distinct from a basic plumage, *regardless of when it is attained.*

Most species with distinct alternate plumages live in relatively harsh, often aquatic, environments (e.g., loons, waterfowl, shorebirds, gulls, and alcids) and/or are long-distance migrants (e.g., many warblers, Scarlet Tanager, and Bobolink). In addition, these are all species that can find the concentrated, rich food resources required to fuel two moults. Other species of open environments, including tubenoses and hawks, have only one moult and plumage per cycle – but these species tend to be apex predators: their food is harder to

find, and perhaps less predictable. Presumably they compensate by investing more energy into producing better quality feathers that will last through a moult cycle. As might be expected, very few resident tropical birds of aseasonal and relatively protected forest environments are known to have alternate plumages. The handful of Neotropical birds that are known to have alternate plumages are mainly birds of exposed habitats in open country, seedeaters, for example. In northern temperate forests with relatively protected environments, most of the resident species, be they woodpeckers or chickadees, also follow the basic-basic-basic pattern.

Prealternate moults can be considered as comprising two or three types. *Facultative Prealternate Moults* are those whereby feathers attained are similar in appearance to those shed (e.g., some flycatchers and wrens). These moults tend to be highly variable in extent, even within a species, and reflect the replacement of feathers that become heavily worn, such as tertials, central rectrices, and some head feathers.

Obligate Prealternate Moults are those whereby feathers attained are obviously different in colour and/or pattern from those they replace e.g., a male Mallard or male Scarlet Tanager. While the original impetus for such moults may have been facultative, subsequent selection has "obliged" these species to undergo more extensive moults than they might need simply to replace a few worn feathers.

Ornamental Prealternate Moults are those whereby feathers attained differ in structure, but not necessarily in colour or pattern, from those they replace, and may be viewed simply as a subset of Obligate Prealternate Moults. In some cases, ornamental alternate feathers may have no equivalent in basic plumage, such as the crests of Double-crested Cormorants, plumes of breeding herons, or the long tail streamers of jaegers.

In a few reported cases, some feathers may be replaced more than twice per cycle, but in general the details of such moults are not well documented, and these need not be considered here. Essentially, any moult strategy we see today involves some modification upon the basic-basic-basic pattern. Armed with this overview of moult, we can look at a couple of representative examples of two common moult strategies.

Red-tailed Hawk. We have to start somewhere, so let's start with the egg. The chick hatches and, in the case of a raptor, undergoes a relatively long nestling period which culminates, after two downy stages, in a strong plumage with which the young Red-tail fledges (its juvenal plumage). This plumage protects the bird through migration and winter, when it learns how to forage. Having survived the winter, and sitting out its first nesting season, the yearling Red-tail takes advantage of the longer days and increased food in summer, when it undergoes a complete moult into fresh basic plumage. In some cases, birds may not have time and/or food enough to complete this moult before migration so they suspend moult over migration and, for example, replace the outer primaries and some other feathers when they reach the winter grounds. And so, moult is fitted into the annual cycle, and Red-tailed Hawks moult from one basic plumage to another.

Blackpoll Warbler. Again, let's start with the egg. A Blackpoll Warbler hatches and after a fairly brief nestling stage with a single, fluffy feather coat (its juvenal plumage), it moults into a plumage very similar in appearance to the adult basic plumage – greenish and dull, perhaps selected for to help birds be inconspicuous to predators when foraging in leafy canopy. This plumage carries the young Blackpoll through migration to South America, where there is plenty of food during the boreal winter. There it undergoes a moult of its head and body again, plus perhaps some upperwing coverts and tertials (i.e., a prealternate moult),

replacing these feathers within only six months or so of fledging. Surely those feathers would last a little longer, so why replace them again in winter? Thinking ahead, after winter the Blackpoll has to undertake a long migration followed by breeding, so that the next time it could "find time" to moult it would be over a year old. By then its feathers probably *would* have become too worn to function, and so a winter moult balances the equation of moult, migration, and breeding. While the original impetus for a prealternate moult may have been functional rather than ornamental, it is completed just prior to the return to the breeding grounds and the ensuing competition for territories and mates. This timing may help explain why evolution has caused male Blackpoll Warblers to upgrade their unassuming winter appearance along with their moderately worn feathers. Then in late summer, after breeding, the Blackpoll takes advantage of plentiful food and undergoes a complete (prebasic) moult before migrating south, the males again incognito. Thus, an alternate plumage is fitted into the annual cycle.

Summary

While moult may seem an overwhelming and bewildering subject when viewing a "messy-looking" moulting bird in the field, the underlying principles of moult are fairly simple. Every bird has to moult, and when and where it moults are inter-related to, and finely balanced with, all other aspects of its life history, in particular breeding and, when relevant, migration. All species have a complete, or near complete, moult once a year, usually after breeding: the prebasic moult producing basic plumage. The prebasic moult occurs when a bird can find sufficient food to fuel the moult: on the summer grounds immediately after breeding; on the winter grounds after fall migration; or in some cases the moult starts on the summer grounds and ends on the winter grounds. A minority of species (in the global sense) fit a second moult into their annual cycle: the prealternate moult producing alternate plumage. Usually this moult involves only some head and body feathers because moult is an energy-demanding process, and to replace an entire plumage twice a year would require a lot of fuel.

In conclusion, any moulting regime is a result of compromise among the demands of a bird's life cycle, and the moult strategies we see today reflect millions of years of evolutionary fine-tuning.

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