A BASIC UNDERSTANDING OF MOULT:
WHAT, WHY, WHEN, AND HOW MUCH?

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Various papers have been written about moult. Those who people formerly confuse basic and alternate plumages (the Humphrey-Parker system) into 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 essay 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 species (e.g., see Pyke 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 expanse of time, selection has favored 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 pieced together, 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 Hofmeyr and Parker (1959, 1963), and it is widely accepted that the Humphrey-Parker system is the most helpful framework for studying moult and plumages. Again, 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.

Where 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 nobody has documented gratuitous moult; birds moult for a reason.

Let’s say a species increases its plumage supply and needs to replace its feathers quickly. So it needs to moult before winter sets in. But it’s a long time before the new moult has grown, and the bird has to moult almost all of its feathers. If it were to moult all of its feathers at once, it would not be able to fly or walk. Instead, it moult a little at a time, and the moult process is speeded up. Moult is often associated with migration.
Let's say a bird evolves, the ancestral bird in a primordial and essentially seasonal 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, time or season context, moult may be essentially an ongoing process without strong seasonal peaks, at least within a species. In fact, some tropical birds in seasonal climates still show year-round patterns of moulding. In particular, though, the replacement of larger feathers demands more energy and, over time, moult cycle may become bound 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 flyshes 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 moultg 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. Moult in fall replaces these worn feathers and provides a cost 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, for example, Least Nighthawks, 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 might stop and then moult as 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 moulding, than the short days of the northern hemisphere fall and winter. In some cases, birds may suspend moult during migration; first, they start to moult before migration, then stop moultng, migrate, and finish moult after migration (e.g., various shorebirds and terns). Furthermore, different populations or age-classes of a species may employ different moulding 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 moultng (Pyle 1997). Thus, a heavily worn Dusky/Hammond's Flycatcher found on fall migration should be a Dusky.
Basic and Alternate Plumas

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 order.

(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 molt 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 borders in the northern hemisphere. These two systems are different, but one is not necessarily better - which you depend 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 moulted from one 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 molt by which it is attained is termed the premolt. 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 molt a year; so does a pigeon, or a woodpecker, or a stork. 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 loon 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 molt, these extra moult become housed to food supply and fit into the bird's annual energy cycle, but in the 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 moult corresponded with the start of the breeding season, then a different-looking plumage might result. Perhaps this could be brighter, or "feminine" than the basic plumage, perhaps more cryptic and better suited for camouflage. Over time, forces such as natural selection 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 premolt moult. Although we tend to associate alternate plumage with breeding plumage this is not a good idea - the term "alternate" is basic and was proposed to free studies of molt from such preconceptions. Thus, an alternate moult is any second moult distinct from a basic moult, 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 Tanagers, and Bobolinks). In addition, these are all species that can find the concentrated, rich food resources required to fuel two mouls. 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 they need expected movements; known to seed-eaters, me basic-basis. Pruned: Prealternate shed (e.g., even with an tertials, Oblig at en col Tanager's selection) simply to Orius, but its rc as a subject have no t plumes of 1 but it is gen esidered by the basic-l represents hatches in minutes, a f juveniles leaves hatching R undergoes time and av migration reach the moult from a after a fall moult of 3 or 4 296 Bitters Journal - Volume 8 No. 5 December 1999 and January 2000
find, and perhaps less predictable. Presumably they compensate by investing more energy into producing better quality feathers that will last through a mouth cycle. As might be expected, very few resident tropical birds of seasonal 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, such as the bee hummingbird of Cuba. For a few days in March, they develop a black and white plumage, with the tail mostly black. The plumage is shed in stages, with the head and neck being the first to change color. The change is followed by the rest of the body, with the wings and tail feathers being the last to change. This is a typical example of a bird that undergoes a complete molt every year. These birds are known for their ability to change color rapidly, often in response to environmental changes. The change in color is thought to be a means of communication among the birds. The black and white plumage is thought to be a way for the birds to blend in with their surroundings, helping them to avoid predators. The change in color is also thought to be a way for the birds to communicate with each other, as the black and white plumage is a unique color combination that helps the birds to be easily recognized by other members of the flock.
replacing their 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 about, after winter the Blackpoll has to undertake a long migration followed by breeding, so that the next time it could "find time" to molt it would be over a year old. By then its feathers probably would have become too worn to function, and so a winter molt balances the equations of molt, migration, and breeding. While the original impetus for a premolt moulting may have been functional rather than ornamental, it is completed just prior to the rains to the breeding grounds and the ensuing competition for territories and mates. This moulting may help explain why evolution has caused male Blackpoll Warblers to upgrade their unwintering summer 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) moulting before migrating south, the males again incognito. Thus, an alternate plumage is fitted into the annual cycle.

Summary

While molt may seem an overwhelming and bewildering subject when viewing a "nonspecy-
looking" warbler bird in the field, the underlying principles of molt are fairly simple. Every bird has to molt, and when and where a molt results 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, molt once a year, usually after breeding; the pre-
basic molt producing basic plumage. The prebasic molt occurs when a bird can find suffi-
cient food to fuel the molt: on the summer grounds immediately after breeding; on the win-
ter grounds after fall migration; or in some cases the molt starts on the summer grounds and ends on the winter grounds. A minority of species (in the global sense) fit a second molt into their annual cycle: the premolt producing alternate plumage. Usually this molt involves only some head and body feathers because molt 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 molt strategies we see today reflect millions of years of evolu-
tionary foot-tumming.

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LITERATURE CITED


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