All You Ever Wanted to Know About Molt But Were Afraid to Ask

Part II: Finding Order Amid the Chaos

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Part 1 of this review (*Birding*, October 2003, pp. 490–496) discussed examples of the seemingly endless variations possible in molt strategies worldwide, relating to when and where a bird molts. These variations come about through the interplay of several underlying factors that can be summarized as: 1) environment and food; 2) breeding and size; and 3) migration. In Part 2 we'll look at how patterns of molting can be identified to reveal some semblance of order amid the apparent chaos. Then we'll review real-life examples and compare the Humphrey-Parkes system (which considers only the number of molts) with the life-year system (which relates plumages and a bird's appearance to seasons).

Molt Terminology

The molt strategies of birds—discussed in Part 1 of this article—are inextricably linked with other aspects of their life histories, such as breeding cycles, food supply, and, in some cases, migration cycles. Traditional terminologies, originating in the temperate regions of Europe or North America, have used terms such as "breeding" or "nuptial" plumages, or "summer" and "winter" plumages. Humphrey and Parkes (1959, 1963) pointed out, however, that for meaningful comparisons to be made among species worldwide, a system of nomenclature for molts and plumages should be free from preconceptions related to other life-history phenomena. Consequently, their 1959 paper introduced a system of nomenclature whereby variations in the patterns of plumage succession may be described, compared, and contrasted among different groups of birds by applying the concept of *homology* to the study of molts.

The defining criterion for homology is common ancestry: Since modern birds presumably share a common ancestor, they should also share a common molt strategy. (*Analogy*, by contrast, reflects convergence through adaptation. For example, human hands and bat wings have homologous bone structures, whereas bat wings and bird wings are analogous adaptations for flight.) In some cases, determining homologies can be problematic, if not impossible (Mindell and Meyer 2001), but observations and syntheses of broad patterns can produce hypotheses regarding presumed homology. The Humphrey-Parkes (H-P) system provides a terminology for such hypotheses and has proved useful in comparative studies of molt.

Although the H-P system is helpful for comparative studies of molt, it is not necessarily the most helpful for field birding. Still, to under-

stand the basics of molt strategies we should start with a review of the H-P system, incorporating some modifications proposed recently by Howell *et al*. (2003) and also summarized by Sibley (2002). Remember, though, that Nature does not fit neatly into boxes, so there will always be exceptions that challenge any rules we try to apply. To focus on exceptions is understandable, but to look at broad patterns that apply to the majority of species may be more meaningful and also helps to identify where exceptions really lie.

The Humphrey-Parkes System

The H-P system is founded upon a few tenets, foremost among which are the following: (1) Only molts produce plumages; that is, a bird can have no more and no fewer plumages than it has molts. (2) The complete (or near-complete) molts of adults can be considered homologous and thus comparable among species. (3) Molts and plumages should be named independently of other phenomena in a bird's life cycle, such as seasons or breeding status. And (4) molts are named for the plumages they produce, not for those they replace. The H-P system was developed with adult birds in mind, and for these birds it works well. In essence, the H-P system is concerned only with the bottom line of how many molts occur, *i.e*., how many times a feather follicle is activated; it does not worry about when or where the molts occur, or about what the resultant plumages look like.

The gist of the H-P system is that the complete (or near-complete) molt can be considered homologous among all adult birds; other plumages have evolved as additions or responses to various types of selection. The H-P system uses the neutral term *Basic Plumage* for this presumed homologous plumage, worn by all birds. This is actually quite an intuitive term: All birds have a basic plumage; it's that basic. In fact, most birds worldwide have *only* basic plumages, and so they molt from one basic plumage to another basic plumage each year (*e.g*., penguins, hawks, hummingbirds, jays, and even many wood-warblers). Hence, in these species, basic plumages encompass both the so-called "summer" and "winter" plumages or the "breeding" and "non-breeding" plumages.

The commonest variation on this basic pattern is the addition of another plumage into the adult cycle. The H-P system calls any second plumage added into the basic cycle an *Alternate Plumage*—it alternates with the basic plumage, and, often, it creates an alternate appearance. An alternate plumage is any second plumage, regardless of when it is attained; often it is equated with "breeding plumage", but this is an oversimplification that can be misleading. In a few cases, another plumage or plumages may be added into the basic cycle in addition to alternate plumage; the H-P system

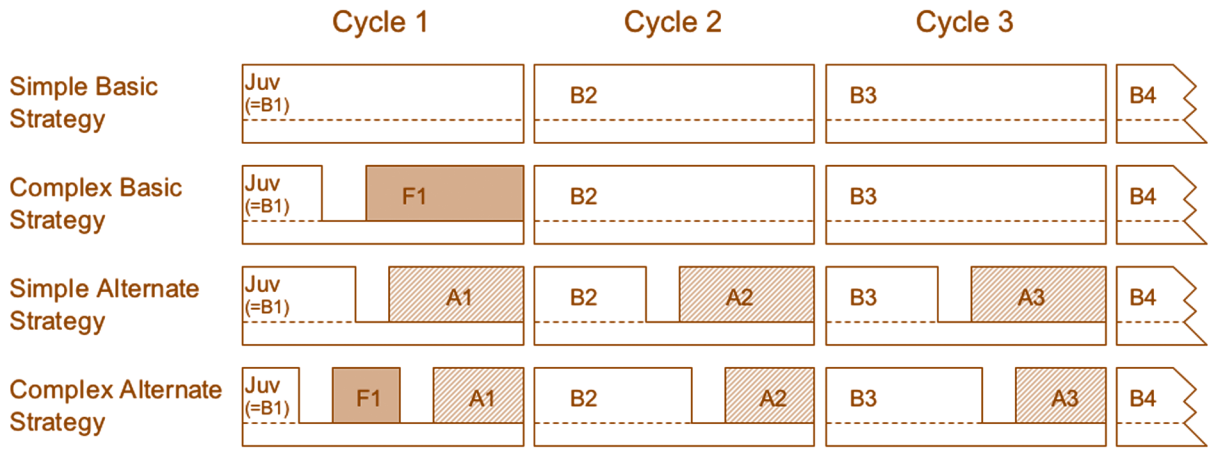


Fig. 1. Diagrammatic representation of underlying molt strategies that build upon the Simple Basic Strategy (SBS): the Complex Basic Strategy (CBS), Simple Alternate Strategy (SAS), and Complex Alternate Strategy (CAS). Juv: Juvenal Plumage (First Basic). F1: Formative Plumage. A1: First Alternate Plumage, *etc*. B2: Second Basic Plumage, *etc*. Molts are indicated symbolically as breaks between plumages and cycles, and the area below the dashed line represents flight feathers (which can be replaced in some F1 and A1 plumages). Note that a cycle extends from the initiation of one prebasic molt to the initiation of the next, and that plumages (and molts) are consistently numbered in reference to the cycle in which they occur. In many CBS and CAS species, note that adult plumage is attained in the second plumage cycle; that is, B2 (and A2) plumage equals adult basic (and alternate) plumage. *From Howell* et al. *2003.*

provides the term *Supplemental Plumage* for these extra plumages, but they are sufficiently rare and poorly documented that we needn't worry about them. Note that basic, alternate, and supplemental refer to plumages, not to molts. The molts by which these plumages are attained are called the *Prebasic Molt*, the *Prealternate Molt*, and the *Presupplemental Molt*, respectively, *i.e.*, the molts that precede, and produce, these plumages.



Fig. 2. All tubenoses— like this De Filippi's Petrel (*Pterodroma defilippiana*)—apparently have a Simple Basic Strategy. How could you identify this bird if you saw it off California? To distinguish it from Cook's Petrel, note the relatively large and stout bill, extensive gray patches at the neck sides, and lack of a distinct black tail tip—*and the conspicuous molt on the wings*. Cook's Petrels molt their primaries from February through August, whereas De Filippi's molt their primaries from November through April. So it is possible that a Cook's Petrel on the date of this photo might have started primary molt, but it would not be as advanced as on this bird. *Off Valparaíso, Chile; 1 February 2000. © Steve N. G. Howell.*

Successive basic (and alternate) plumages, if they can be distinguished by color or pattern (as in immature gulls, for example), are called second basic, second alternate, third basic, and so on, until adult plumage is attained. One other H-P term you should be aware of is *Definitive*, which refers to any plumage (basic or alternate) that no longer changes in appearance with age. Hence, definitive plumage usually equates with what is commonly termed "adult" plumage.

The original H-P system considered the first postjuvenal plumage as the so-called "first basic plumage", and this marked the start of their system for naming basic plumages. The frequent similarity in appearance of the first basic and adult basic plumages was presumably responsible for this conclusion, but this seems to be little more than the legacy of equating first winter and adult winter plumages in traditional systems. Howell *et al.* (2003) argue that these similarities are analogous, not homologous, and they propose instead that it is more logical for plumage nomenclature to start with juvenal plumage. *Juvenal Plumage* is defined as a bird's first covering of "true" (*i.e.*, pennaceous or non-downy) feathers, and it tends to be the plumage in which a bird fledges. A bird's juvenal plumage is a fixed point that is more likely to be homologous among species than the highly variable molt by which some or all juvenal plumage is replaced. Birds in juvenal plumage can still be called juveniles, but this stage should be recognized as synonymous with first basic plumage. The first plumage cycle of a bird then extends from juvenal plumage to the start of the second prebasic molt, which occurs at about one year of age in most birds. Under the conventional H-P system the first cycle begins with the start of the so-called first prebasic molt, which can happen any time in the first year or two of a bird's life, depending on the species involved; this complication leads to inconsistencies in naming and comparing plumages that are beyond the scope of this paper. Readers interested in



Fig. 3. Formative plumage in many species looks much like adult basic plumage, as is the case with the Hooded Warbler. This individual looks like a classic "adult male" (*i.e.*, in basic plumage—Hooded Warblers molt only once a year), but the relatively brown-looking alula feathers (visible at the bend of wing) suggest that this individual is, in fact, an immature in formative plumage. However, distinguishing between these two plumages in the field, or from photos, is difficult, and the safest course is to leave the age unknown. *Upper Texas Coast; April 2001. © Brian E. Small.*

the thoughts behind this revision are referred to Howell *et al*. (2003) for more information.

When this adjustment (considering juvenal plumage synonymous with first basic plumage) is made to the original H-P system, four underlying patterns of plumage replacement can be identified that apparently encompass all species of birds (Fig. 1); these patterns were first identified, and named provisionally, by Howell and Corben (2000b). In terms of increasing complexity these four patterns are termed the *Simple Basic Strategy* (called the Primitive Basic Strategy by Howell and Corben 2000b and by Sibley 2002), the *Complex Basic Strategy* (also called the Modified Basic Strategy), the *Simple Alternate Strategy*, and the *Complex Alternate Strategy*. The first two strategies relate to birds that have only basic plumages as adults, and the second two to those that also have alternate plumages added into the adult cycle. The differences within the two basic strategies and within the two alternate strategies occur only in the first cycle, after which molts are repeated in a pattern like that of the adult (Fig. 1).

Before we look at these strategies, a question arises: If juvenal plumage is synonymous with first basic plumage, what do we now call the so-called first basic plumage of the original H-P system? Howell *et al*. (2003) propose the term *Formative Plumage*, attained by a *Preformative Molt*, for any plumage that is present in the first plumage cycle but that lacks a homologous counterpart in subsequent plumage cycles. Consequently, the traditional first basic plumages of many species are now termed formative plumages, *i.e.*, unique, first-cycle plumages analogous, but not homologous, with adult basic plumages. In essence, formative plumages are novel plumages worn by a bird in its first year of life as it catches up to the adult cycle of regular, stereotyped molts (for examples, see below under explanation of the Complex Basic Strategy).



Fig. 4. Most large gulls follow the Simple Alternate Strategy. This first-cycle Thayer's Gull is largely in juvenal plumage but has started its first prealternate molt on the mantle, scapulars, and sides of the breast. Note the fresher, grayer, and slightly contrasting new feathers. *Puerto Peñasco, Sonora, Mexico; 22 January 2003. © Steve N. G. Howell.*

The Simple Basic Strategy (SBS). This is the simplest possible molt strategy and consists only of a single basic plumage per cycle (Fig. 1). This pattern of plumage succession is relatively uncommon, being found primarily in some large, long-lived seabirds (*e.g.*, penguins, tubenoses; Fig. 2) that nest on islands traditionally free from predators, as well as in larger raptors that have relatively few predators. These species have relatively long chick or nestling stages during which the young grow a strong juvenal (first basic) plumage. Most or all individuals of these species do not breed in their first year, and their second prebasic molt typically commences earlier than that of breeding adults.

The Complex Basic Strategy (CBS). This strategy applies to species in which a preformative molt (traditionally termed first prebasic) is added into the first cycle but in which no added molt occurs in subsequent cycles (Fig. 1). The preformative molt replaces whatever feathers presumably need to be replaced in order for a bird to survive its first year and enter into the adult cycle. The CBS is found in a wide range of species, from kestrels and kingfishers to woodpeckers and waxwings. One reason for the frequent occurrence of CBS may be that juvenal plumage grows during the breeding season, while adult prebasic molts generally follow the breeding season. Consequently, the first cycle is usually slightly longer than adult cycles, and juvenal plumage would have to be at least as durable as adult basic plumage if it were to be retained throughout

the first cycle. But juvenal plumage is generally of poorer quality than subsequent basic plumages. One possible reason for this, for example in passerines, is that nestbound young are often susceptible to predation, and so they grow a functional, but not necessarily durable, juvenal (first basic) plumage with which they can leave the vulnerability of the nest. Subsequently they undergo a variably extensive, preformative molt by which they attain stronger feathers that protect them until the start of the second prebasic molt. The preformative molt often includes only head and body feathers (as in many passerines), or it can be complete (as in hummingbirds); it can even vary considerably in extent within a species, as discussed in Part 1. The formative plumage that results often looks much like the adult basic plumage (Fig. 3).



Fig. 5. Most small sandpipers, such as this Black Turnstone, have a Complex Alternate Strategy. But is this bird molting from formative plumage to first alternate plumage, or from definitive basic to definitive alternate plumage? Birders should be aware that no single system of molt terminology is "the best"; some terminologies apply better in the field, and others make more sense from an evolutionary standpoint. *Bodega Harbor, California; April 1999. © Steve N. G. Howell.*

The Simple Alternate Strategy (SAS). This strategy applies to species in which only a single plumage (traditionally termed first basic and mistakenly believed to comprise two plumages) is added into the first cycle, and one plumage (alternate) is added into subsequent cycles. The added first-cycle molt usually appears to be homologous with the prealternate molt of adult cycles (Howell *et al.* 2003; Fig. 1). This strategy is relatively uncommon and was recognized only recently (Howell and Corben 2000a). The SAS has been identified mainly in relatively large, aquatic non-passerines, namely loons, pelicans, some sea ducks, and some large gulls (Fig. 4). In some groups, *e.g.*, ducks and large gulls, the evolution of the SAS may have come about through loss of a second first-cycle molt (i.e., derived from the Complex Alternate Strategy, discussed below). As a rule, species following the SAS do not breed in their first year, so a single molt may be adequate to help them survive through their first cycle; that is, there is no need for two molts, as there is in species with the Complex Alternate Strategy.

The Complex Alternate Strategy (CAS). This strategy applies mostly to species in which two plumages are added into the first cycle, while one added plumage occurs in adult cycles (Fig. 1). Such species include many shorebirds, small gulls, and apparently all passerines that have alternate plumages as adults. One first-cycle molt (the conventional first prebasic molt) lacks a counterpart in the definitive cycle and is now termed a preformative molt. As in CBS species, preformative molts vary in extent from partial to complete and typically produce plumages that look much like adult basic plumages (Fig. 5). Usually, the second plumage added into the first cycle appears to be homologous to the adult alternate plumage (Fig. 1). Shared life-history traits of many CBS species are that they are migratory and that most breed, or may attempt to breed, in their first year; some combination of these factors has presumably produced this molt strategy. In mostly non-migratory species, such as grouse and nuthatches, life-history characteristics such as the wear of plumage in exposed and scrubby habitats, or the abrasion of head feathers by sticking faces into tree cavities, may have caused these extra molts to evolve.

Table 1 (after Howell *et al.* 2003) classifies North American bird families by these four categories and helps to make sense out of the seemingly wide variety of molting regimes discussed in Part 1 of this article. For example, note that all passerines follow only two strategies—CBS and CAS. But note also that many areas of uncertainty remain in the simple field of descriptive molt studies. When looking at a species whose molt is undescribed (*e.g.*, Fig. 6), we now have only four options to consider as starting hypotheses—or two choices if we know whether the subject has an alternate plumage as an adult.

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	SBS	CBS	SAS	CAS
NON-PASSERINES				
Loons			●	
Grebes				●
Albatrosses	●			
Petrels and Shearwaters	●			
Storm-Petrels	●			
Gannets and Boobies	●			
Pelicans			?	?
Cormorants			●	
Anhingas		?	?	
Frigatebirds	?	?		
Herons and Egrets		○	●	?
Ibises and Spoonbills		●	●	?
Storks	?			
Vultures	●			
Whistling-Ducks		●		
Geese		●		
Ducks			●	●
Hawks	●	○		
Falcons	●	○		
Chachalacas		●		
Grouse		●		●
New World Quail		●		○
Rails and Coots		●	?	●
Limpkin		?	?	
Cranes	?	?		
Plovers			?	●
Oystercatchers		?	?	●
Stilts and Avocets			?	●
Sandpipers		○	○	●
Skuas and Jaegers			?	●
Gulls	○		●	●
Terns			?	●
Auks		?	●	●
NEAR-PASSERINES				
Pigeons and Doves		●		
Cuckoos		●		

	SBS	CBS	SAS	CAS
Barn Owls	●			
Typical Owls		●		
Nightjars		●		
Swifts	?	●		
Hummingbirds		●		
Trogons		●		
Kingfishers	?	●		
Woodpeckers		●		
PASSERINES				
Tyrant-flycatchers		●		●
Shrikes		?		●
Vireos		●		●
Crows and Jays		●		
Larks		●		
Swallows and Martins		●		○
Titmice and Chickadees		●		
Verdin		●		
Bushtits		●		
Nuthatches		●		●
Creepers		●		
Wrens		●		○
Dippers		●		
Kinglets		●		?
Thrushes		●		○
Wrentit		●		
Mockingbirds and Thrashers		●		?
Starlings		●		
Pipits and Wagtails				●
Waxwings		●		
Olive Warbler		●		?
Wood-warblers		●		●
Tanagers		●		●
Sparrows and allies		●		●
Grosbeaks and Buntings		●		●
Blackbirds and Orioles		●		●
Finches		●		●
Weaver Finches		●		

Table 1 (after Howell *et al*. 2003). Molt strategies of North American birds categorized by family or subfamily. Legend: SBS = Simple Basic Strategy; CBS = Complex Basic Strategy; SAS = Simple Alternate Strategy; and CAS = Complex Alternate Strategy. Dark circles (●) denote the predominant molt strategy or strategies within a family (>35% of species), and light circles (○) denote a less-frequent strategy or strategies (<35% of species). A question mark indicates that the molt strategy may occur but that confirmation is needed.

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Real-life Examples

Having worked through the theory of different molt strategies, let's look at some real-life examples of how particular species relate to these four strategies (and see Figs. 1 and 7).



Fig. 6. The molt strategy of the South Georgia Pipit (*Anthus antarcticus*), which breeds in the subantarctic Atlantic Ocean, has not been studied. But because all passerines follow either the Complex Basic Strategy or the Complex Alternate Strategy, we can predict that this little-known species will prove to have one of these two strategies. *Albatross Island, South Georgia; 26 March 2002. © Steve N. G. Howell.*

• ***Simple Basic Strategy:*** *Sharp-shinned Hawk.* We have to start somewhere, so let's start with the egg. The chick hatches and undergoes a nestling period of 4–5 weeks that culminates, after two downy stages, in a strong juvenal (first basic) plumage in which the young Sharp-shin fledges. This plumage protects the bird through migration and winter, when it hones its foraging techniques. Having survived the winter, and sitting out its first nesting season, the yearling Sharp-shin takes advantage of the longer days and increased food in summer, when it undergoes a complete molt into second basic plumage before migrating south for the winter. From here on, the Sharp-shin migrates north in spring, nests, starts its prebasic molt while still nesting, and completes it before fall migration. And so molt is fitted into the annual cycle, with Sharp-shinned Hawks molting simply from one basic plumage to another.

• ***Complex Basic Strategy:*** *Eastern Towhee.* Like many passerines, towhees hatch mostly naked (they have some vestigial, wispy down on their upperparts). They quickly molt into a fairly weak but functional juvenal (first basic) plumage that allows them mobility, so that they can leave the nest within 10–11 days of hatching (or even 7–8 days if disturbed; Greenlaw 1996). Taking advantage of late-summer flushes of food, they then replace their juvenal head and body feathers plus upperwing coverts with a stronger, formative plumage similar in appearance to the adult basic plumage. Some individuals, especially of southern populations that hatch earlier and experience stronger environmental ultraviolet radiation, also replace some to all of the tertials and central rectrices—that is, the feathers that protect the closed secondaries and tail (Pyle 1997). Formative plumage is worn through the next breeding season and then replaced in late summer and fall by the complete second prebasic molt into adult plumage, after which birds undergo only a single (prebasic) molt per year.

• ***Simple Alternate Strategy:*** *Herring Gull.* When Herring Gulls hatch, they wear a downy plumage that protects them for the first few weeks of life and under which a strong juvenal plumage develops. The juvenal (first basic) plumage is mostly full grown in 5–6 weeks after hatching, and birds fledge mainly in August and September. The prealternate molt out of juvenal plumage is highly variable in timing and starts in most birds sometime between October and February (Howell *et al.* 1999). Some individuals (especially in populations breeding on the East Coast) undergo a fairly extensive prealternate molt of head, body, and scapular feathers by midwinter, while others (apparently from high-latitude breeding populations) undergo almost no prealternate molt before their first spring (Howell 2001). The complete second prebasic molt starts in April and May, about two months earlier than that of breeding adults, and usually ends by October. The second prealternate molt often starts in October, before the second prebasic molt has finished, and the molting schedule is then similar to that of an adult—with complete prebasic molts from July to December and overlapping partial prealternate molts from October to April.

• ***Complex Alternate Strategy:*** *Scarlet Tanager.* In this species the almost-naked hatchling quickly grows a fairly weak but functional juvenal plumage that allows it to leave the vulnerability of the nest. It then takes advantage of plentiful late-summer food and replaces its juvenal head and body feathers plus upperwing coverts with a stronger, formative plumage similar in appearance to the adult basic plumage. This plumage carries the young tanager through migration to South America, where there is plenty of food during the boreal winter. There, like the adults, it undergoes a prealternate molt of its head and body feathers, plus perhaps some upperwing coverts, tertials, and rectrices (Pyle 1997), replacing these feathers within only

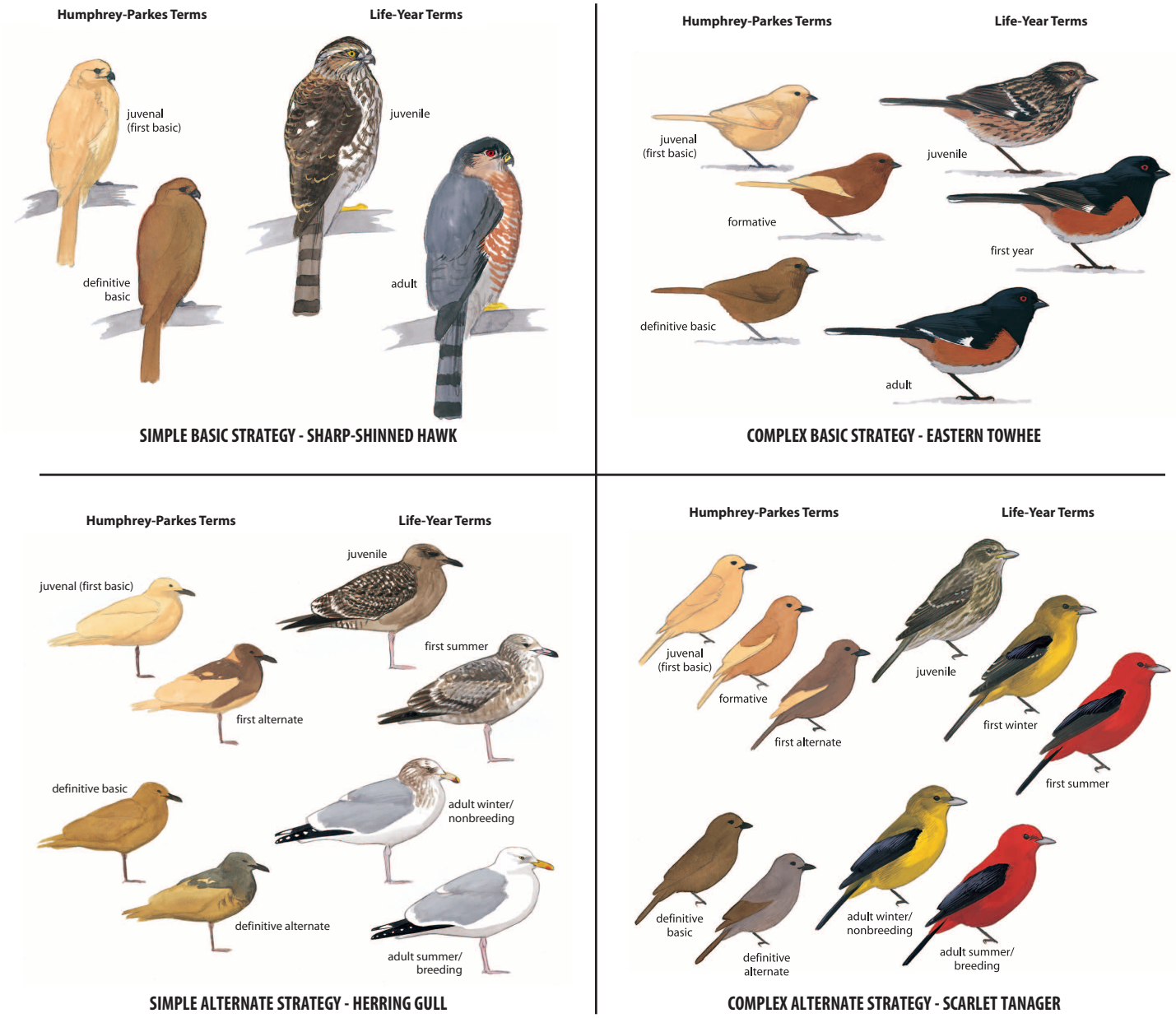


Fig. 7. Shown here is a comparison of Humphrey-Parkes (H-P) and life-year terms. Note that the H-P system is concerned only with the number of molts, whereas the life-year system emphasizes the appearance of the bird (see also Fig. 1). These systems are discussed in greater detail in the text. *From* Sibley's Birding Basics *by David Allen Sibley; © 2003 by David Allen Sibley. Reprinted with permission from Alfred A. Knopf, a division of Random House, Inc.*

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 Scarlet Tanager 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 formative feathers could have become too worn to function, and so a winter molt balances the equation of molt, migration, and breeding. Thus, an alternate plumage as well as a formative plumage fit into the first cycle. After this first cycle, molts follow the adult pattern of a complete prebasic molt in fall and a partial prealternate molt in late winter and spring.

The Humphrey-Parkes System *vs.* the Life-Year System

As we have seen, the H-P system looks simply at molts and helps us to organize and compare patterns of molt and plumage sequence among different species. The life-year system describes the appearance of a bird as we see it in the field—which does not necessarily relate to the

pattern of underlying molts. Some things to think about when trying to equate H-P molts and plumages with what we see in the field are the duration of molts, the possible overlap of successive molts (*i.e.*, a new molt can start before the previous one has finished), the potential for plumage to change in appearance over the course of a single molt (*e.g.*, hormone changes that control color may not always correspond to periods of molting), and the potential for plumage to change appearance due to wear rather than to molt.



Fig. 8. This first-cycle California Gull shows at least two different patterns in its postjuvenal (first alternate) scapulars: Most of the shorter scapulars have dark centers and broad, abraded pale edges, whereas many of the longer scapulars are fresher and plain-gray overall. Such differences presumably reflect hormonal changes that relate to color patterns; they do not represent two different molts but simply different stages in a single, protracted molt. *Puerto Vallarta, Jalisco, Mexico; 5 January 2003. © Steve N. G. Howell.*

Complete (prebasic) molts in most passerines tend to be fairly short in duration and to last for at most 2–3 months. In North American species, these molts typically are discrete events that occur in fall: either between the end of the breeding season and the start of winter for residents, or before and after fall migration for migrants. In larger species, however, with their more numerous and larger feathers, molts can be much more protracted (*e.g.*, the complete prebasic molt in large gulls can take 5–6 months). And in birds with alternate plumages the prealternate molt can start before the prebasic molt has finished, so that periods of molting overlap. In some cases it can be difficult, if not impossible, to distinguish between prebasic and prealternate molts: For example, do scapular feathers molted by an adult Herring Gull in October mark the end of its prebasic molt or the start of its prealternate molt? Without knowing the history of every feather follicle—and how many times it has been activated—this question is not easily answered. These protracted molts mean that some large birds rarely hold a given plumage *per se* for very long. For example, large gulls in winter have often started their prealternate molt in fall, so winter adults aren't really in basic plumage, as we often tend to think.

Another point to bear in mind is that the color and pattern of new and incoming feathers relates largely to the hormonal state of the bird. This means that the "breeding plumage" of a sandpiper that is not in breeding condition in the summer months (as occurs with some first-year birds) can look just like its "winter" or "non-breeding" plumage (Chandler and Marchant 2001). Thus, the use of color and pattern in trying to name plumages should be approached carefully. Similarly, the color and pattern of feathers can change over the course of a single

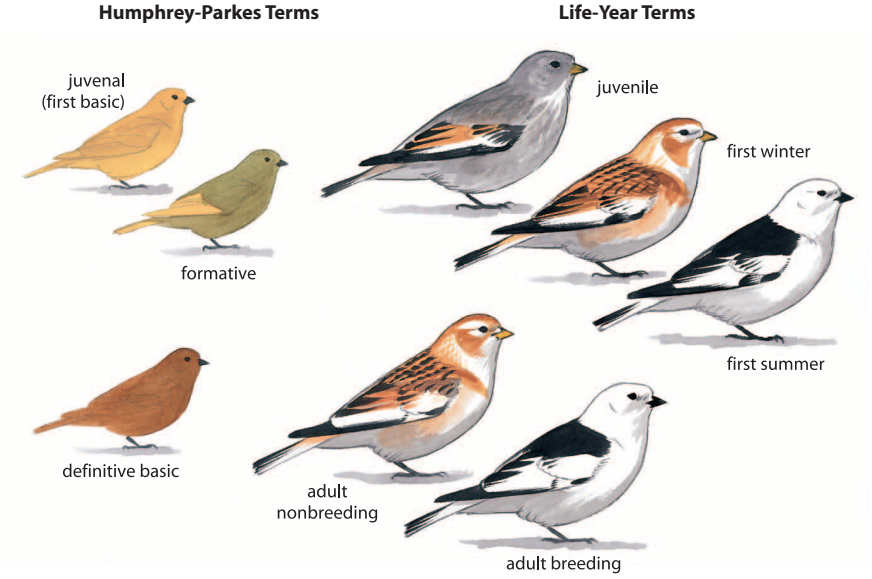


Fig. 9. Shown here is a comparison of Humphrey-Parkes terms and life-year terms for the Snow Bunting, which has a Complex Basic Strategy. Note that the marked seasonal changes in appearance are due to wear, and not to molt. *From* Sibley's Birding Basics *by David Allen Sibley; © 2003 by David Allen Sibley. Reprinted with permission from Alfred A. Knopf, a division of Random House, Inc.*

molt, particularly a protracted molt such as occurs in first-year large gulls: First-alternate feathers attained in fall tend to be brownish overall, while first alternate feathers attained later in the molt are more often grayish overall, presumably due to hormonal changes (Fig. 8). These different feather patterns help explain why some first-year gulls have often been assumed to have two molts.

And then there are differences in appearance that can be brought about simply by the wearing off of feather tips to reveal underlying plumage patterns. This is a less energy-costly way of changing appearance than molt, and it is quite common in passerines. Willoughby *et al*. (2002) recently showed that wear is responsible for the seasonally changing appearance of Lawrence's Goldfinch; previously it was presumed to have two molts (Pyle 1997). A well-known and more readily seen example is the European Starling, where the pale spots of "non-breeding" plumage wear off to produce the glossy "breeding" plumage—but it is all the same basic plumage in the H-P system. An even more dramatic example of changing appearance due to wear (rather than to molt) is found in the Snow Bunting: The striking differences between a fresh-plumaged fall bird and a breeding male in mid-summer are caused by the wearing off of pale-buff feather tips to reveal the glossy-black feather bases, and not by molt. Thus, if we equate life-year terms with H-P terms (and this is a good example of why simply switching terms doesn't work), the Snow Bunting's bright "breeding" plumage is in fact its heavily worn "winter" plumage (Fig. 9). And in the field it may not be possible to distinguish between a first-year Snow Bunting in formative plumage and an adult in basic plumage—yet the life-year system allows us to describe them both as wearing "non-breeding plumages". In fact, the Snow Bunting's molt strategy is Complex Basic, just as with Eastern Towhee, but we might not guess this simply from watching birds in the field.

As is so often the case, these two systems are different, but one is not necessarily better: Which you use depends on your purpose. For studies of molt, the H-P system is the only useful way to compare species and evaluate molt strategies. But for field birding it is fine to use terms such as "adult", "first-winter", "breeding plumage", and so on. In fact, trying to apply H-P terms to birds in the field implies a precision that may be spurious (due to the factors discussed above).

A practical compromise for birders who aspire to more precision may be to age birds by plumage cycles, which often equate to years and, in most North American species, correspond to periods between molts of the primary feathers. This approach avoids the problem of what we mean, for example, by a "second year" Herring Gull seen in February. Does this mean a bird in its second calendar-year (and about 7 months old), or is it a bird in its second winter of life (and about 19 months old)? A first-cycle Herring Gull in February means the former, while a second-cycle Herring Gull means the latter. Cycles also get around the problem of different seasons between hemispheres, or on the Equator, and are something to consider when describing birds in the field.

Does Understanding Molt Help Us in the Field?

It's all very well to have an understanding of molt, but does it have any practical value? In short, Yes. Here are a couple of examples of how molt can help in identification, and potentially even in conservation, based simply upon my observations on memorable Memorial Day pelagic trips off North Carolina this past spring. Many of the Band-rumped Storm-Petrels that occur off North Carolina apparently come from "winter-breeding" populations in the eastern Atlantic, because presumed adults off North Carolina in late May were molting their middle and outer



Fig. 10. Apart from its intrinsic interest, the study of molt may have important consequences for understanding bird biology and conservation. In the case of the Black-capped Petrel, for example, an index of reproductive success could be developed by carefully noting the relative numbers of fresh-plumaged juveniles to worn-plumaged and/or molting (shown here) adults. *Off Hatteras, North Carolina; Late May 2003. © Steve N. G. Howell.*

primaries—a very conspicuous field mark when you look for it. By contrast, Leach's Storm-Petrels breed in the northern summer and do not molt primaries in May. Thus, any Band-rumped/Leach's Storm-Petrel with obvious wing molt was a Band-rumped—a field mark visible at greater distance than the conventional plumage marks. Being able to identify a Band-rumped more quickly meant calling it out sooner, so that more people could see it. However, juvenile Band-rumpeds from the most recent breeding season were in fresh plumage and not molting, so this was only a one-way field mark: A Band-rumped/Leach's Storm-Petrel without wing molt could have been either species.

And molt might help in other ways, such as in monitoring population trends. Adult and non-breeding immature Black-capped Petrels in late May are either in worn plumage (and just about to start wing molt) or, more likely, in wing molt (Fig. 10). But newly fledged juveniles are in fresh plumage, with no wing molt. By carefully noting the proportion of fresh-plumaged juveniles to worn-plumaged and molting birds, an index of breeding success could be developed; over a period of ten or twenty years, the data could be useful for monitoring and conservation.

Summary

While molt may seem like an overwhelming and bewildering subject, the underlying principles are fairly simple: Every bird has to molt, and when and where it molts reflects food availability balanced with other aspects of its life cycle, in particular breeding and, when relevant, migration. All species have a complete (or near-complete) molt once a cycle, usually after breeding: the prebasic molt producing basic plumage. A minority of species (in the global sense) fit a second molt into their annual cycle: the prealternate molt 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.

By divorcing molt and plumage terminology from preconceptions relating to seasons or breeding status, it is possible to recognize broad, underlying patterns of feather replacement that are informative for comparative studies of molt. All birds follow one of four molt strategies: Simple Basic, Complex Basic, Simple Alternate, and Complex Alternate. But from the point of view of field birding it is still helpful to refer to adults and immatures, breeding and non-breeding plumages, *etc*. For species with multiple years of immature plumage it can be helpful to apply the concept of cycles, which avoid the potential ambiguity of some other terms.

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