A COMMENTARY ON MOLT AND PLUMAGE TERMINOLOGY: IMPLICATIONS FROM THE WESTERN GULL

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ABSTRACT: The Humphrey–Parkes system of molt nomenclature takes as the starting point of cyclic plumage succession the highly variable molt that replaces juvenal plumage, entailing inconsistency. If all "postjuvenal" molts are called prebasic, homology between so-called first basic and second basic plumages of birds the same age is lost. We suggest that the juvenal plumage be considered synonymous with first basic plumage, and we define the first basic plumage cycle as the period between the acquisition of juvenal (= first basic) plumage and the acquisition of the second basic plumage. Consequently, the traditional first basic plumage of birds with a single molt and plumage per cycle (e.g., Procellariiformes) should be renamed the second basic plumage; that of species with more complex molt strategies should be considered as a variable, inserted plumage not homologous with a basic plumage. In this way, consistent nomenclature for all prebasic molts and basic plumages of all species can be achieved, regardless of whether additional plumages have been inserted into the basic cycle. We define four strategies that incorporate most if not all known molt strategies and show how these build on the primitive basic strategy, taking juvenal (= first basic) plumage as a homologous starting point.

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 birds. Their far-sighted system remains standard for molt studies in North America, although they acknowledged that "parts of our fundamental thesis [may] need to be altered or broadened" (Humphrey and Parkes 1959: 17). On the basis of our studies of molt in the Western Gull (*Larus occidentalis*) (Howell and Corben 2000), we re-evaluated their molt and plumage nomenclature as applied to large gulls and other large birds in their first year of life. We suggest here a refinement of the H–P system, one that allows for a consistent nomenclature for prebasic molts and basic plumages of all species, regardless of whether or not additional plumages have been inserted into the basic cycle. This consistency is absent from conventional H–P nomenclature, in which equivalent plumages of birds the same age are not always given the same name, as in the disparity between so-called first basic and second basic plumages of birds the same age.

CONVENTIONAL INCONSISTENCY

Particularly in species with alternate plumages, a satisfactory and consistent system for bridging the period between juvenal plumage and definitive basic plumage has been lacking. For example, under conventional terminology, the first complete molt of a Northern Fulmar (*Fulmarus glacialis*) or Red-tailed Hawk (*Buteo jamaicensis*) when about a year old produces a *first* basic plumage, yet the homologous complete molt of a Western Gull produces a *second* basic plumage (Figure 1). American Kestrels (*Falco*

Figure 1. Approximate molting periods over the first four years of life for the Northern Fulmar (NOFU), Red-tailed Hawk (RTHA), and Western Gull (WEGU). Solid blocks, prebasic molt; hatched blocks, prealternate molt. Prebasic molt in the first year (into first basic plumage, as defined here) is the acquisition of juvenal plumage (see text). When molts are viewed in this manner, all second and subsequent prebasic molts can be considered homologous. Data for the fulmar from Cramp and Simmons (1977) and Ginn and Melville (1983), for the hawk from Palmer (1988) and Preston and Beane (1993), for the gull from Howell and Corben (2000).

sparverius) have a partial molt in their first winter, whereas Merlins (*Falco columbarius*) do not (Palmer 1988). Thus a year-old kestrel is undergoing its second prebasic molt while a Merlin of the same age is undergoing its first. Some Glaucuous-winged Gulls (*L. glaucescens*) have an extensive molt in their first winter, while others appear to have no molt of juvenal feathers prior to their complete prebasic molt when a year old (Howell, pers. obs.). Thus the prebasic molt of some year-old Glaucous-winged Gulls is their first while for others it is their second.

This discord is contrary to one of the H–P system's four criteria for a semantically clean terminology for plumage and molt: "the nomenclature must be consistent" (Humphrey and Parkes 1959: 14). Yet while all of the species noted above have fundamentally similar molt strategies (Figure 1), the nonhomologous terminology has not been questioned. We suggest this inconsistency can be remedied.

DEFINITIONS

We follow Humphrey and Parkes (1959: 24) in supposing that "plumages were not originally sexually, seasonally, or developmentally dimorphic" and that "primitive or ancestral plumages were most likely renewed periodically and completely by protracted molts." Similarly, we believe it reasonable to consider the ancestral molt strategy to be the simplest possible, similar to that manifested today by birds such as the Procellariiformes (e.g., Northern Fulmar) and most Falconiformes (e.g., Red-tailed Hawk), which have only a single (i.e., basic) plumage per cycle. This we term the *primitive basic strategy*. We consider the molts present in the primitive basic strategy to be present in all species and believe these are the only molts that should be considered prebasic. Any other molts in species with more complex strategies should be considered as additions to the primitive basic strategy.

A key point here is the definition of "basic plumage," a term coined by Humphrey and Parkes (1959:15) for the *adult plumage* that is "almost invariably lost and renewed by a complete molt." From this adult basic plumage Humphrey and Parkes worked *backward* to juvenal plumage without critically addressing the issue of what has been called first basic plumage.

Concerning the prebasic molt, then, Humphrey and Parkes (1959: 15) stated "although complete in 'adults,' this molt may be either complete or partial in young birds undergoing postjuvenal feather replacement." Thus they regarded any "postjuvenal" molt as a prebasic molt, whether partial, incomplete, or complete. For birds with a primitive basic strategy (e.g., Procellariiformes; Figure 1) this is logical, but Humphrey and Parkes (1959) provided no explanation why any molt immediately following juvenal plumage should be a prebasic molt, especially in birds with more than one plumage per cycle. Presumably they considered that any development of plumages should start from a basic plumage, a premise with which we agree in principle.

Thus the H–P system takes its starting point as the attainment of first basic plumage, effectively naming a plumage (first basic) after the molt that introduces it. This is contrary to other H–P usage, in which the name of a molt is derived *from* the plumage it produces. Having a highly variable "postjuvenal" molt as the starting point immediately introduces inconsistencies in comparisons of plumage homologies: if all "postjuvenal" molts are called prebasic molts, homology between so-called first basic and second basic plumages of birds the same age is lost.

A critical point in evaluating plumage homologies should be a consistent and workable definition of a bird's *first basic cycle*, yet this seems not to exist. Viewing plumages and molts in terms of cycles is an extremely powerful means of interpretation. Humphrey and Parkes (1959: 3) explained that a "cycle ... is to be understood as a shortened version of 'plumage cycle;' a cycle (in an adult bird) runs from a given plumage or molt to the next occurrence of the same plumage or molt." Therefore, a cycle could be viewed as a basic cycle (i.e., between basic plumages) or an alternate cycle (i.e., between alternate plumages), but in either case the cycle also includes other cyclic phenomena in a bird's life, such as breeding and migration. The H–P cycle was defined in terms of an individual adult bird, but it can also be considered largely synonymous with the cycle of a species or population whose members share a common breeding season, as in the great majority of temperate-zone species, in which case "cycle" is synonymous with annual cycle.

Obviously, the starting point in life is not repeated in a cyclic manner for an individual bird, yet this event is a fundamental part of the cycle of all species. We suggest that the first basic plumage cycle can be defined as the period between the attainment of juvenal plumage and the acquisition of the next basic plumage via a complete, or nearly complete, molt that corresponds to a molt present in the primitive basic strategy (see Figure 2). This is in accord with the H–P definition of a cycle, and this first cycle then becomes comparable among all species in the same way that a definitive plumage cycle is comparable. As a rule, the first basic cycle has a duration similar to the definitive basic cycle.

THE PROBLEM OF "FIRST BASIC"

Under the H–P system, some species have a complete so-called "first prebasic molt" within a few months of hatching. At first sight these molts appear homologous with the definitive prebasic molt because they produce

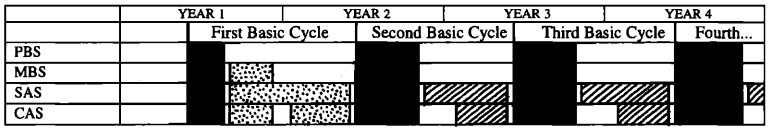

Figure 2. Diagrammatic representation of molt strategies that build on the primitive basic strategy (PBS): the modified basic strategy (MBS), simple alternate strategy (SAS), and complex alternate strategy (CAS). Solid blocks, prebasic molts; stippling, molts inserted into the first cycle; hatching, prealternate molts in the second and subsequent cycles. See text for further explanation of these strategies. Note that a basic cycle extends from the acquisition of one basic plumage to the acquisition of the next.

a similar-looking plumage. Complete molts are not necessarily prebasic, however, and before naming any complete molt one should examine the molts of closely related species and also consider how a molt fits into a species' life history.

In *Calidris*, for example, the "postjuvenal" molt is incomplete to complete in the Little Stint (*C. minuta*), partial to incomplete in the Red-necked Stint (*C. ruficollis*), and partial in the Western Sandpiper (*C. mauri*) (Prater et al. 1977, Cramp and Simmons 1983). Thus the traditional "complete first prebasic molt" of a Little Stint is simply one end of a continuum rather than homologous with the adult's complete prebasic molt. Passerines with traditional "complete first prebasic molts" are generally species whose habits entail a high degree of feather wear, e.g., the Wrentit (*Chamaea fasciata*) in chaparral or the European Starling (*Sturnus vulgaris*) nesting in cavities. In some cases, the "postjuvenal" molt varies from partial to complete within a single species, e.g., the Phainopepla (*Phainopepla nitens*; Pyle 1997), providing a strong argument that this molt is not homologous with the definitive complete prebasic molt but instead reflects an adaptation to environmental conditions.

Consequently we suggest there is no good reason to call any "postjuvenal" molt within the first cycle a prebasic molt, no matter how much the resulting plumage may resemble the definitive basic plumage. When the first basic cycle is defined as we have done, all so-called "first prebasic molts," other than those of species with a primitive basic strategy, can be viewed as inserted into the first basic cycle (see Figure 2).

Understandably, perhaps, the similarity of these molts and plumages to those of the adult has masked their homology, but the H–P system was developed to allow the recognition of homologies independent of preconceptions derived from characters such as the appearance of a plumage or the season of its acquisition.

CONSISTENT BASIC HOMOLOGIES

There are two options for aligning terminology among all species. The first is to consider the complete prebasic molt at the end of a bird's first cycle always to be the first prebasic molt, as done currently for a Northern Fulmar or Red-tailed Hawk. This would involve major upheaval in terminology for all

species with alternate plumages (e.g., many Anseriformes, Charadriiformes, and Passeriformes). The second option is to call the complete molt at the end of the first cycle a second prebasic molt, as is done presently for species with inserted plumages. This would require a change in terminology for species following the primitive basic strategy (e.g., Procellariiformes and most Falconiformes). We believe that the molt strategy of a Western Gull suggests a logical approach to resolving this problem.

Howell and Corben (2000) described the molt cycles and sequences of the Western Gull in California and concluded that from a bird's first fall into spring it undergoes only a single protracted molt; there is no evidence that any feathers are replaced more than once. By comparison with the adult cycle, this first partial molt of a Western Gull, out of what is traditionally termed juvenal plumage, appears homologous with a prealternate molt, not with a prebasic molt as has been previously thought (Figure 1; also see Figure 1 of Howell and Corben 2000). Other large gulls and large wading birds also follow this strategy (Johnston 1956, Kushlan and Bildstein 1992). Presumably it had been overlooked because the single molt is protracted, the appearance of feathers of the same generation can vary with time of replacement, and, perhaps, the tradition that fall molts are prebasic, spring molts prealternate (Howell and Corben 2000).

If one considers the Western Gull's first partial molt a first prealternate molt, it follows that its juvenal plumage could be considered equivalent to a first basic plumage. This may seem radical, but there is logic in a terminology for plumage succession that starts with the young bird rather than with the definitive prebasic molt of an adult. Beyond inferring the synonymy of the juvenal and first basic plumage from the Western Gull, we offer the following arguments in favor of this proposal.

At the most fundamental level, juvenal plumage is a bird's first "basic" plumage, although it may not have been defined strictly as such. In some orders (e.g., Sphenisciformes, Gaviiformes, Procellariiformes), the so-called juvenal and subsequent basic plumages are remarkably similar, supporting their homology. Selective pressures operating differently on different species, however, could modify the juvenal plumage greatly. In the Passeriformes, the juvenal plumage of most species can be viewed as a highly modified first basic plumage, perhaps a "quick and dirty" plumage to get immobile, vulnerable young out of the nest.

Juvenal plumage is also attained by a complete molt (the traditional prejuvenal molt), completeness being the single unifying characteristic of homologous prebasic molts recognized by the H–P system. The molt into juvenal plumage occurs, by necessity, via a more temporally compressed and more synchronous process than for subsequent basic plumages.

Juvenal plumage is widely defined as the plumage in which a bird fledges, and all authors have agreed that juvenal plumage among most if not all birds is comparable. For this reason, juvenal plumage was taken by Humphrey and Parkes (1959) as the starting point for the development of basic plumages. We have simply reinterpreted the starting point. It is somewhat paradoxical that in proposing a system to disconnect terminology from a bird's life cycle, Humphrey and Parkes purged the term "adult" and replaced it with "definitive" yet retained the terms "juvenal" and "juvenile," perhaps

the most fundamental links with a bird's life cycle. Instead, it might have been quite logical to start by calling the juvenal plumage a first basic plumage. We suspect, though, that the spell of traditional nomenclature, which the H–P system sought to replace, was too strong for this homology to be recognized. Our reinterpretation of first basic plumage is simply a validation of the flexibility and utility of the H–P system.

If juvenal plumage is considered equivalent to a first basic plumage, then traditional second basic plumage for all species with inserted plumages can still be termed second basic plumage. In species following the primitive basic strategy, however, the traditional first basic plumage (acquired when the bird is one year old) needs to be renamed the second basic plumage, and so on. This is a relatively minor change, yet it allows for a system of consistent nomenclature for all prebasic molts and basic plumages of all species, regardless of whether additional plumages have been inserted into the basic cycle (Figures 1, 2). That is, plumages are numbered in reference to the cycle in which they occur, so that the fourth basic plumage of one species will always be comparable to the fourth basic plumage of any other species.

If so desired, the traditional juvenal plumage can still be called "juvenal" (and birds in this plumage "juveniles"), but it should be recognized as *synonymous with first basic plumage*, so that it can be followed by prealternate and/or presupplemental molts.

MOLT STRATEGIES

Following juvenal (i.e., first basic) plumage, a bird molts however necessary to get through its first basic cycle and enter into a cycle like that of an adult. While the variety of "postjuvenal" molts may seem overwhelming, all molt strategies involving plumages inserted into the first cycle are variations of three fundamental patterns of plumage development that build upon the primitive basic strategy of a single prebasic molt per cycle (Figure 2).

The Modified Basic Strategy. Many species, especially passerines (e.g., Corvidae, Vireonidae), have a unique molt and plumage inserted into the first basic cycle (the traditional first prebasic molt and first basic plumage) but no inserted molt in the adult cycle (Figure 2). This molt ranges from being limited to a few feathers to complete.

The Simple Alternate Strategy. This is the strategy of large gulls and some wading birds, in which the single inserted molt of the first cycle appears homologous with the prealternate molt of the adult cycle (Figure 2).

The Complex Alternate Strategy. In some cases two molts and plumages have been inserted into the first cycle (e.g., most small gulls, *Calidris* sandpipers): the traditional first basic and first alternate plumages (Figure 2). The inserted molts in such cases usually involve a partial to, rarely, complete molt, followed by a partial molt. Exceptionally, three molts may be inserted into the first cycle, as in the Indigo Bunting (*Passerina cyanea*; Rowher 1986).

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LITERATURE CITED

Cramp, S., and Simmons, K. E. L. (eds.). 1977. Handbook of the Birds of Europe, the Middle East, and North Africa, vol. 1. Oxford Univ. Press, Oxford, England.

Cramp, S., and Simmons, K. E. L. (eds.). 1983. Handbook of the Birds of Europe, the Middle East, and North Africa, vol. 3. Oxford Univ. Press, Oxford, England.

Ginn, H. B., and Melville, D. S. 1983. Moult in Birds. BTO Guide 19. Br. Trust Ornithol., Tring, England.

Howell, S. N. G., and Corben, C. 2000. Molt cycles and sequences in the Western Gull. W. Birds 31:38–49.

Humphrey, P. S., and Parkes, K. C. 1959. An approach to the study of molts and plumages. Auk 76:1–31.

Johnston, D. W. 1956. The annual reproductive cycle of the California Gull I: Criteria of age and the testis cycle. Condor 58:134–162.

Kushlan, J. A., and Bildstein, K. L. 1992. White Ibis (*Eudocimus albus*), in The Birds of North America (A. Poole and F. Gill, eds.), no. 9. Acad. Nat. Sci., Philadelphia.

Palmer, R. S. 1988. Handbook of North American Birds, vol. 5. Yale Univ. Press, New Haven, CT.

Prater, A. J., Marchant, J. H., and Vuorinen, J. 1977. Guide to the Identification and Ageing of Holarctic Waders. Br. Trust Ornithol., Tring, England.

Preston, C. R., and Beane, R. D. 1993. Red-tailed Hawk (*Buteo jamaicensis*), in The Birds of North America (A. Poole and F. Gill, eds.), no. 52. Acad. Nat. Sci., Philadelphia.

Pyle, P. 1997. Identification Guide to North American Birds, Part 1. Slate Creek Press, Bolinas, CA.

Rowher, S. A. 1986. A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. Auk 103:281–292.

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