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THE FIRST BASIC PROBLEM: A REVIEW OF MOLT AND PLUMAGE HOMOLOGIES

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Abstract. All birds have fundamentally similar patterns of plumage succession. Thus Humphrey and Parkes (1959) proposed a system of nomenclature (the H-P system), based on homologies, that has become standard for molt studies in North America. However, presumably analogous similarities in pattern between first basic and definitive basic plumages have obscured homologies. Many plumages conventionally known as "first basic" are better considered as novel first-cycle plumages that lack homologous counterparts in subsequent cycles. Consequently, current nomenclature does not consistently reflect between-species homologies. Howell and Corben (2000b) proposed that traditional juvenal plumage can be considered an unambiguous starting point for a terminology that better reflects presumed homologies in basic plumages; alternate and other nonbasic plumages may not necessarily be homologous between species. Four underlying strategies of increasing complexity incorporate all known patterns of plumage succession: the Simple Basic Strategy, the Complex Basic Strategy, the Simple Alternate Strategy, and the Complex Alternate Strategy. We review inconsistency in the H-P system; explain the four underlying strategies; and discuss how one can identify homologies (if any) between plumages in first and subsequent cycles and among taxa. Many species have novel plumages added into their first plumage cycle; we argue that existing terminology for these plumages is unsuitable and we term them *formative plumages* attained by *preformative molts.* Finally, we provide examples of how this modified H-P system can be applied to diverse taxa of birds while reflecting the homology underlying all basic plumage cycles. Our revision validates the flexibility and utility of the H-P system.

Key words: Complex Alternate Strategy, Complex Basic Strategy, formative plumages, molt terminology, plumage succession, Simple Alternate Strategy, Simple Basic Strategy.

El Problema del Primer Plumaje Básico: Una Revisión de las Homologías de la Muda y del Plumaje

Resumen. Todas las aves tienen patrones de sucesión del plumaje fundamentalmente similares. De este modo, Humphrey y Parkes (1959) propusieron un sistema de nomenclatura (el sistema H-P), basado en homologías, el cual ha sido de uso común en estudios de muda de plumaje en Norte América. Sin embargo, supuestas similitudes análogas entre el primer plumaje básico y el plumaje definitivo básico han confundido las homologías. Muchos plumajes convencionalmente conocidos como "primer básico" son considerados mejor como plumajes originales del primer ciclo que carecen de contrapartes homólogas en los ciclos siguientes. Consecuentemente, la nomenclatura actual no refleja las homologías entre especies. Howell y Corben (2000b) propusieron que el tradicional plumaje juvenil puede ser considerado como un punto de partida inequívoco para una terminología que refleje mejor las homologías presuntas en los plumajes básicos; los plumajes alternos y otros plu-

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majes no básicos pudieran no ser homólogos entre especies. Cuatro estrategias de creciente complejidad incorporan todos los patrones conocidos de sucesión de plumajes: La Estrategia Básica Simple, La Estrategia Básica Compleja, La Estrategia Alterna Simple, y La Estrategia Alterna Compleja. Examinamos ciertas inconsistencias en el sistema H-P; explicamos las cuatro estrategias subyacentes, y discutimos cómo se pueden identificar homologías (cuando existen) entre los plumajes del primer ciclo y de los ciclos siguientes, y entre taxa diferentes. Muchas especies tienen plumajes originales adicionales en su primer ciclo de plumaje; sostenemos que la terminología actual para estos plumajes es inadecuada y los denominamos como *plumajes formativos,* logrados por *mudas preformativas.* Finalmente, damos ejemplos de como este sistema H-P modificado puede ser aplicado a diversos tipos de aves y al mismo tiempo reflejar la homología subyacente a todos los ciclos de plumajes básicos. Nuestra revisión valida la flexibilidad y utilidad del sistema H-P.

INTRODUCTION

Molting (the normal and regular growth of feathers, by which plumages are attained) is one of the most important processes in the life cycle of every bird. Despite this, molt remains a relatively little-studied subject in ornithology (Thompson and Leu 1994, Rohwer 1999), and the physiological and environmental processes governing molt in wild birds are poorly understood (Voitkevich 1966, Payne 1972). It has long been recognized, however, that all bird species have fundamentally similar patterns of plumage succession, and descriptive accounts of plumage cycles exist for many species worldwide.

The molt strategies of birds are inextricably linked with other aspects of their life history, such as breeding cycles, food supply, and, in some cases, migration cycles. Traditional terminologies 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, 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, but determining this can be problematic, if not impossible (Mindell and Meyer 2001). Nonetheless, observations and syntheses of broad patterns can produce hypotheses regarding presumed homology, which can then be tested. The so-called Humphrey-Parkes (H-P) system provides a terminology for such hypotheses and has proved useful in comparative studies of molt.

The H-P system is founded upon a few tenets, foremost among which are (1) that only molts produce plumages; that is, a bird can have no more and no fewer plumages than it has molts; (2) that the complete (or near-complete) molt of adults can be considered homologous and thus comparable across species; (3) that molting is a cyclic phenomenon (most, but not all, species' life-history cycles correspond to an annual cycle, but chronological age *per se* is not a criterion for making comparisons among species); (4) that molts and plumages should be named independently of other phenomena in a bird's life cycle, such as seasons or breeding status; and (5) that molts should be named on the basis of the plumage they produce, not on the basis of the plumage they replace. The H-P system is standard for molt and plumage studies in North America, although some have questioned its practicality (e.g., Willoughby 1992). Any system that attempts to draw lines on natural processes will be imperfect—Nature does not sleep in a Procrustean bed—but it is widely accepted that the H-P system is the most practical for studying molt and plumage succession (Rohwer et al. 1992, Thompson and Leu 1994).

In view of accumulating data, Howell and Corben (2000a, 2000b) identified and addressed an inconsistency in the H-P system: the noncorrespondence between nomenclature and presumed homology in so-called first basic plumages. Here we review current misuse of, and inconsistency in, the conventional H-P system; pursue the implications of Howell and Corben's (2000b) reinterpretation by explaining the four underlying molt strategies they identified; and summarize how these strategies apply to all North American and Australian bird families (representing a diverse spectrum of species with which we are familiar). We also define and name plumages and molts inserted into the first cycle;

discuss how one may identify presumed homologies (if any) between plumages in first and subsequent cycles and across taxa; and provide case studies to illustrate how this modified H-P system reflects presumed homology in all basic plumages. This revised framework of first-cycle molts and plumages defines a more useful starting point for addressing questions about the evolution of molt strategies, and about potential molt and plumage homologies.

MISUSE OF THE HUMPHREY-PARKES SYSTEM

Readers are referred to Humphrey and Parkes (1959) for a full explanation of their system, but the gist is that the plumage attained by adult birds in their complete (or near-complete) molt (which usually repeats on an annual cycle) may be considered homologous across species; other plumages have evolved as additions in response to various types of selection. This presumed homologous plumage shared by all birds is termed basic plumage. Any second plumage added into the basic plumage cycle is termed an alternate plumage, which usually involves molt of only head and body feathers (i.e., not including all remiges and rectrices).

Conceptually brilliant, yet theoretically simple, the H-P system has been frequently misused, despite valiant attempts to clarify its usage by Rohwer et al. (1992) and Thompson and Leu (1994). Examples of misuse abound. For Trumpeter Swan (*Cygnus buccinator*), Mitchell (1994) treated the plumage sequence as juvenal to first alternate to definitive basic, while for the Tundra Swan (*C. columbianus*) Limpert and Easton (1994) considered the sequence as juvenal to first basic to definitive basic. For the Rock Ptarmigan (*Lagopus mutus*), Holder and Montgomerie (1993) described a plumage sequence running from supplemental to basic to alternate, while the White-tailed Ptarmigan (*L. leucurus*) plumage sequence is reported to run from basic to supplemental to alternate (Braun et al. 1993). Both swans and both ptarmigans undoubtedly have homologous plumage sequences, so why the confusion in terminology when using an inherently simple system? Indeed, even Rohwer et al. (1992) and Thompson and Leu (1994) disagreed over how one should name first-year plumages of certain *Passerina* buntings with a view to recognizing so-called homologous plumages.

A crux of the H-P system is how one recognizes homologies. Rohwer et al. (1992:298) advocated that molt homologies be determined by comparing "the timing, extent, and color change in each molt with that of closely related species that have already been described." This approach may reveal homologies among closely related species, but if the patterns of plumage succession already described have been founded on an arbitrary point of reference (see below), then broader patterns of homology could be obscured. Consequently, conventional methods of determining homologies might under-represent the potential of the H-P system. To recognize potential molt homologies it seems more helpful to identify and compare patterns of plumage succession across a broad range of taxa.

WHY THE CONFUSION?

Misuse of the H-P system results largely from a combination of three factors: (1) an inherent inconsistency relating to the starting point of nomenclature for plumage succession; (2) a failure to divorce plumage color and pattern from an evaluation of homologies; and (3) widespread misconception that the H-P plumage terms basic and alternate are simply synonyms for traditional nonbreeding (or winter) and breeding (or summer) plumages, respectively.

The inherent inconsistency stems from the H-P system taking its starting point of cyclic plumage succession as the highly variable molt that replaces juvenal plumage with so-called first basic plumage. A consequence of this is an arbitrary first cycle which, depending on species or even individuals, can start at any time over the course of a bird's first year or two of life (Fig. 1A). Humphrey and Parkes (1959) provided no explanation why the molt immediately following juvenal plumage should be a prebasic molt. Presumably they considered that any development of plumages should start from a basic plumage, a premise with which we agree in principle. It appears, however, that the perceived equivalence (based largely on phenotypic similarity of color and pattern) of traditional adult non-nuptial and first non-nuptial plumage was extended, by analogy rather than any evident homology, to the equivalence of definitive basic and first basic plumage in the H-P system (Humphrey and Parkes 1959).

Similarities in the color and pattern of plumages could, understandably, cloud an apprecia-

tion of homologies. The physiological processes that govern feather pigmentation and molt timing are independent, however, although usually they are coincident (Voitkevich 1966). Thus feather pigmentation is a superficial—and not infallible—criterion for identifying molt homologies. Examples of the independence of feather coloring and molt timing range from wading birds (Beebe 1914) and ducks (Oring 1968), to ptarmigan (Dwight 1900), large gulls (Howell 2001a), and passerines (Herremans 1999). The last example is particularly sobering for those who advocate plumage color or pattern as a criterion by which to identify homologous molts. The Black-chested Prinia (*Prinia flavicans*) has two complete molts per year, and males typically molt from a bright alternate plumage to a dull basic plumage. However, if environmental conditions become suitable for breeding during or just before the prebasic molt, males can molt from bright alternate plumage into an apparently identical bright basic plumage, or into a variably intermediate basic plumage (Herremans 1999).

Certain first-cycle plumages (especially the conventional first basic plumage of most Passeriformes and Charadriiformes) resemble definitive basic plumages in appearance. We contend that these first-cycle plumages are for the most part analogous, not homologous, with basic plumages of subsequent cycles, and that the resemblances in color simply reflect similar dynamics between hormones and pigmentation. The great variability in the extent and timing of many conventional first prebasic molts among and within species (discussed under Complex Basic Strategy, below) lends support to the premise that these first-cycle molts are not homologous with definitive prebasic molts (Howell and Corben 2000b).

By following the evolutionary scenario of ancestral plumages outlined below, it becomes apparent that a fundamental difficulty in applying H-P nomenclature to the conventional first cycle is the absence of a prebasic molt that is homologous across or even within species (Fig. 1A). That is, the conventional first prebasic molt can be complete, fairly extensive, very limited, or, as argued by Howell and Corben (2000a) for the Western Gull (*Larus occidentalis*) and other large gulls, not present at all. This clearly causes problems for conventional H-P nomenclature because if the first cycle has to be fixed from the start of the "first prebasic molt" and a conventional first basic plumage is absent, then in its stead some other plumage will be named first basic.

DEFINING THE FIRST PLUMAGE CYCLE

There is something of a catch-22 here: the inconsistency in conventional H-P nomenclature is clearly illustrated by redefining the first plumage cycle, but a logical pathway to redefining the first cycle can only be appreciated when one recognizes that there is an inconsistency in the present system. Howell and Corben (2000b) addressed this issue by two logical steps: (1) assuming the ancestral molt strategy is the simplest possible; and (2) defining juvenal plumage as the first basic plumage.

We agree with Humphrey and Parkes (1959: 24) that "plumages were not originally sexually, seasonally, or developmentally dimorphic" and that such "primitive or ancestral plumages were most likely renewed periodically and completely by protracted molts." We also agree with Howell and Corben (2000b:51) that it is most parsimonious "to consider the ancestral molt strategy to be the simplest possible, similar to that manifested today by birds such as Procellariiformes . . . and most Falconiformes . . . which have only a single (i.e., basic) plumage per cycle." We term this hypothesized ancestral pattern of plumage succession the Simple Basic Strategy (SBS); Howell and Corben (2000b) named it the Primitive Basic Strategy. Molts corresponding to those present in the Simple Basic Strategy occur in all birds and, it seems reasonable to conclude, *are the only molts that should be considered homologous across all species* (Fig. 2). Thus, SBS molts comprise simply a single complete or near-complete prebasic molt once per cycle, and each cycle starts with a prebasic molt (e.g., Northern Fulmar [*Fulmarus glacialis*] and Red-tailed Hawk [*Buteo jamaicensis*] in Fig. 1). Any other molt strategy can be viewed as building upon the Simple Basic Strategy by the addition of extra molts into the basic plumage cycle.

A plumage cycle (often shortened simply to cycle) "runs from a given plumage or molt to the next occurrence of the same plumage or molt" (Humphrey and Parkes 1959:3). Thus, plumage cycles can be basic cycles or alternate cycles, depending on which plumage is treated as the first plumage in the cycle. We use plumage cycle, or cycle, to mean a basic plumage

(A)

	Year 1 J F M A M J J A S O N D	Year 2 J F M A M J J A S O N D	Year 3 J F M A M J J A S O N D
Northern Fulmar	PJ	PB1	PB2
Red-tailed Hawk	PJ	PB1	PB2
Merlin (European)	PJ PB1	PB2	PB3
Merlin (New World)	PJ	PB1	PB2
Glaucous-winged Gull	PJ PB1	PB2	PA2 PB3
Glaucous-winged Gull	PJ	PB1	PA1 PB2

(B)

	Year 1 J F M A M J J A S O N D	Year 2 J F M A M J J A S O N D	Year 3 J F M A M J J A S O N D
Northern Fulmar	PB1	PB2	PB3
Red-tailed Hawk	PB1	PB2	PB3
Merlin (European)	PB1 PF1	PB2	PB3
Merlin (New World)	PB1	PB2	PB3
Glaucous-winged Gull	PB1 PA1	PB2	PA2 PB3
Glaucous-winged Gull	PB1	PB2	PA2 PB3

FIGURE 1. Diagrammatic comparison of molt cycles of Northern Fulmar, Red-tailed Hawk, European and New World Merlins, and two strategies of Glaucous-winged Gull. (A) illustrates conventional inconsistency of nomenclature in traditional first prebasic (PB1) and second prebasic (PB2) molts both between and within taxa. Shaded zone represents conventional first plumage cycle. Note how presumed homologies are not reflected when numbering prebasic molts and plumage cycles. PJ = prejuvenal molt; PA1 = first prealternate molt, etc. (B) illustrates revised H-P nomenclature that reflects between-species homology in prebasic molts and cycles. Shaded zone represents revised first plumage cycle. PB1 equates to PJ. PF1 = preformative molt.

cycle. The H-P cycle was defined in terms of an individual adult bird, but it can also be considered equivalent to the cycle of a species or population whose members share a common breeding season. In most cases, even for species of tropical environments, the plumage cycle is an annual cycle (Prys-Jones 1982, Stutchbury and Morton 2001). 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 life cycle of all species. Consequently, following Howell and Corben (2000b), we define the first plumage cycle 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 in the Simple Basic Strategy. Thus, as a rule, the first cycle has a duration similar to subsequent basic cycles (Fig. 2, 3).

We acknowledge that treating juvenal plumages as homologous is an assumption that may prove false; these may simply be analogous plumages based on a widely shared function. A critical review of prejuvenal downy plumages could be helpful in this regard. Most bird species have one such plumage while some reportedly have two (e.g., penguins; Marchant and Higgins 1990). Some species apparently lack prejuvenal downs (e.g., most woodpeckers hatch naked and molt directly into juvenal plumage; Winkler and Christie 2002), whereas kiwis hatch wearing juvenal plumage (Marchant and Higgins 1990). These examples suggest that environmental and life-history traits affect the timing of acquisition of juvenal plumage, but the problem of analogy versus homology remains. For example, birds with long nestling periods are those reported to have two downs. Has juvenal plumage in these species become modified into a second down, or has the prolonged nestling period caused a novel second down to evolve? Pending satisfactory answers to such questions, treating juvenal plum-

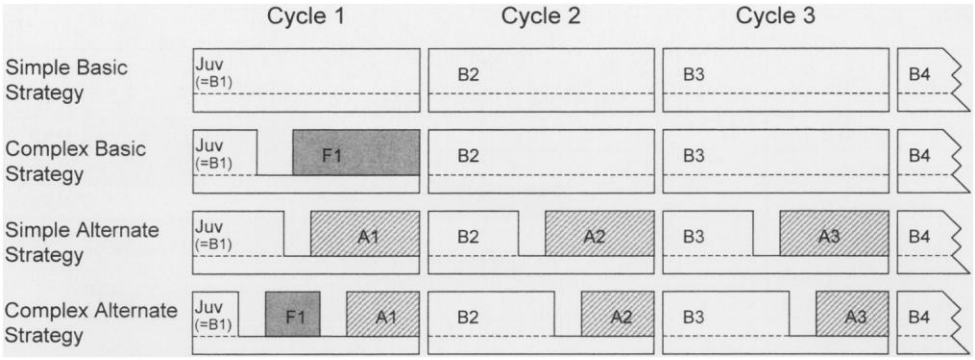


FIGURE 2. Diagrammatic representation of underlying molt strategies that build upon the Simple Basic Strategy (SBS; e.g., Procellariidae): the Complex Basic Strategy (CBS; e.g., Corvidae), Simple Alternate Strategy (SAS; e.g., some large gulls), and Complex Alternate Strategy (CAS; e.g., *Calidris* sandpipers and small gulls). Following Humphrey and Parkes (1959), 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; this consistency is absent from traditional nomenclature (cf. Fig. 1A). In the first cycle, a few CBS and CAS species may have a second preformative molt; and CAS species can have an additional (presupplemental) molt inserted into all cycles (cf. Fig. 4). Juv = Juvenal Plumage (= First Basic); F1 = Formative Plumage; A1 = First Alternate Plumage, etc; B2 = Second Basic Plumage, etc.

ages as homologous is a useful approach to recognizing broad patterns of plumage development in birds (e.g., Table 1).

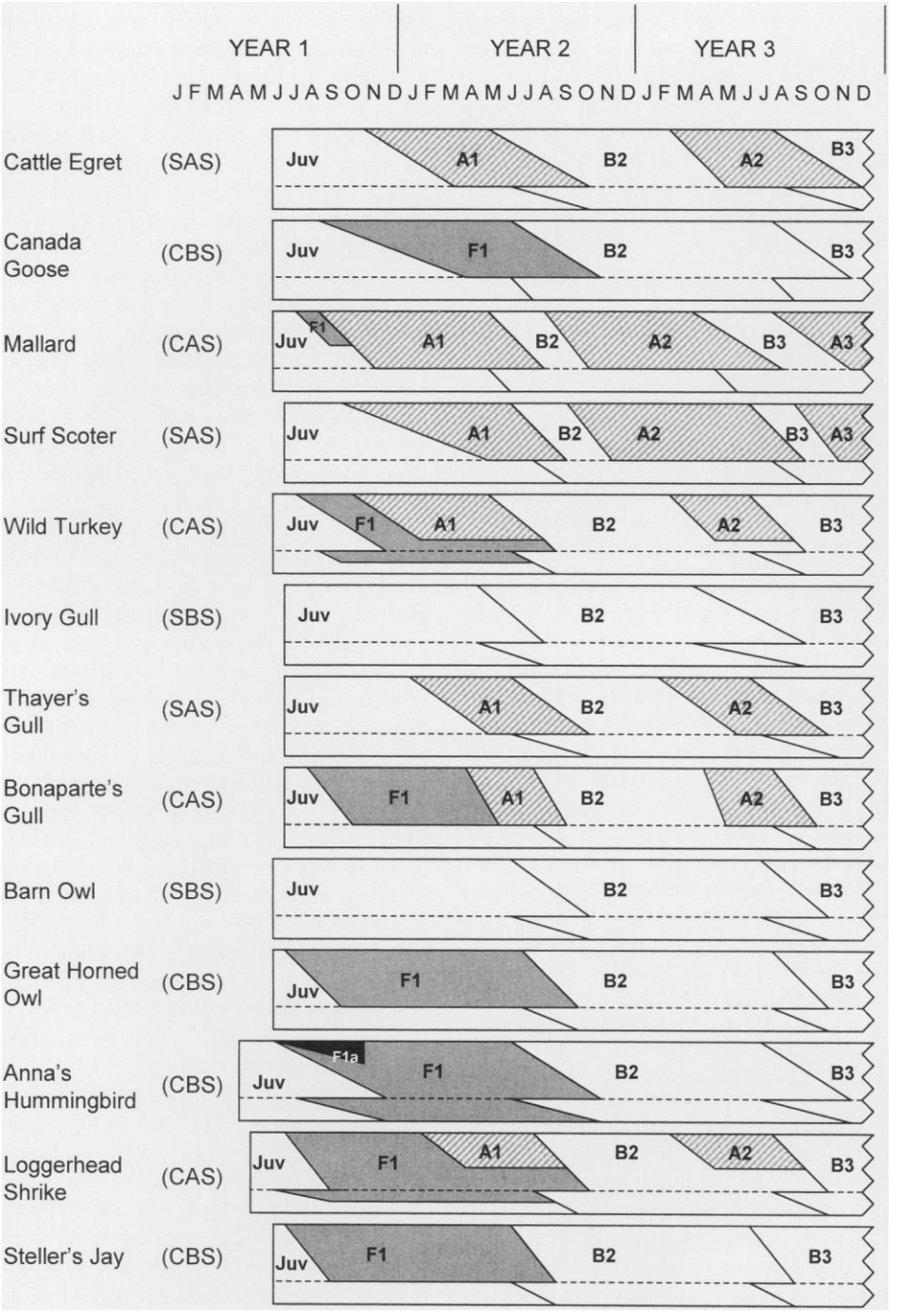
INCONSISTENCY IN THE HUMPHREY-PARKES SYSTEM

Once an unambiguous first plumage cycle is defined, examples of inconsistency in the conventional first cycle (and consequent nomenclature) are easily identified. For example, Marchant and Higgins (1993) reported that the "first prebasic molt" in Pacific Bazas (*Aviceda subcristata*) and Black-shouldered Kites (*Elanus axillaris*) varies from complete to partial, yet these complete and partial molts are quite different: all individuals undergo the complete molt at the end of their first cycle, while some individuals also have an earlier partial molt inserted into the first cycle. Merlins (*Falco columbarius*) in the Palearctic, American Kestrels (*Falco sparverius*), and individuals of some large gull species (*Larus*) have a partial molt in their first fall and winter prior to the complete prebasic molt at the end of their first cycle; Merlins in the Nearctic and other individual large gulls lack this partial molt (Temple 1972, Cramp and Simmons 1980, Palmer 1988b, Forsman 1999, Howell 2001a). Thus, under conventional H-P terminology, some Black-shouldered Kites, some Pacific Bazas, some Merlins, all American Kestrels, and some large gulls attain a second basic plumage via a complete prebasic molt that corresponds to an SBS molt, while the surely homologous complete prebasic molt of some kites, bazas, Merlins, and gulls produces a first basic plumage (Fig. 1A).

Essentially, when using conventional H-P nomenclature, some species (or even individuals) gain an extra "basic" plumage relative to the Simple Basic Strategy and, as a consequence, the facility of comparison is lost (Fig. 1A). Rohwer et al. (1992:299) identified a similar problem of noncorresponding first basic and second basic plumages with Willoughby's (1986) interpretation of first-cycle plumages in *Aimophila* sparrows, and noted that "between-species homologies are lost in the definitive cycle"; however, they did not comment that the same dis-

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FIGURE 3. Diagrammatic examples of revised molt nomenclature for selected species (see Case Studies). Anna's Hummingbird (*Calypte anna*), Loggerhead Shrike (*Lanius ludovicianus*), and Steller's Jay (*Cyanocitta stelleri*), used by Humphrey and Parkes (1959) to illustrate their three major patterns of postjuvenal feather



replacement, involve only two strategies. Molts are represented by diagonal lines between plumages and indicate average timings for species in North America. The area above the dashed line represents head and body feathers, the area below the dashed line flight feathers. Divisions within the vertical scale indicate approximate extents of a molt when it does not involve all feathers (e.g., the molt producing F1 in Mallard does not involve all head and body feathers). Plumage abbreviations follow Figure 2; numbers refer to plumage cycles. SBS = Simple Basic Strategy; CBS = Complex Basic Strategy; SAS = Simple Alternate Strategy; CAS = Complex Alternate Strategy.

crepancy exists in a wider context (e.g., between a hawk and a shorebird, or even within some species; Fig. 1A). When one considers juvenal plumage or definitive basic plumage there is no ambiguity. Yet if one follows conventional H-P nomenclature, the term "first basic plumage" is ambiguous and arbitrary. This is contrary to one of the H-P system's four criteria for a semantically clean terminology: "the nomenclature must be consistent" (Humphrey and Parkes 1959:14). We suggest that it is preferable, and possible, to name plumages such that (1) the second basic plumage of one species corresponds to the second basic plumage of all other species; and (2) plumages are numbered in reference to the cycle in which they occur (with cycles based on the SBS).

PROPOSED REVISION TO HUMPHREY-PARKES NOMENCLATURE

If one accepts that molts corresponding to those in the Simple Basic Strategy are the only molts that should be considered prebasic, that color and pattern can be misleading, and that first cycle molts need not be homologous with molts in subsequent cycles, an order that was missing reveals itself (Table 1). Our reinterpretation adheres to the tenets of the original H-P system except for the classification of many conventional first basic plumages. This may seem a relatively minor, almost semantic, difference, but it is significant in terms of identifying potentially homologous molts and understanding the evolution of molt strategies.

ALIGNING PLUMAGE CYCLES

Once inconsistency in conventional H-P nomenclature is accepted, one is faced with the question of how to align cycles among species. Two options present themselves, as discussed by Howell and Corben (2000b). The first is to consider the complete prebasic molt at the end of a bird's first cycle to always be the first prebasic molt, as is done conventionally with species that follow the Simple Basic Strategy (e.g., Procellariiformes and most Falconiformes). This would result in a major upheaval of conventional terminology (e.g., for all Passeriformes). The second option is to consider the complete prebasic molt at the end of a bird's first cycle the second prebasic molt, as done conventionally with species that have plumages added into the SBS. This would require a change in terminology only for the relatively few species following the SBS.

Clearly, fixing the start of the first plumage cycle is a critical point for any nomenclature. Because the basic plumage cycle is a fundamental characteristic of all species, Humphrey and Parkes (1959) considered that any development of plumage nomenclature should start from a basic plumage. Like workers before them, Humphrey and Parkes (1959) focused on adult birds and worked backward from the relatively simple, stereotyped adult molts to juvenal plumage; thus they equated traditional first winter plumages with first basic plumages and generated the inconsistency detailed earlier. We believe it is more useful for a nomenclature to start from a fixed, nonarbitrary landmark rather than from a moving target.

For several reasons, taking juvenal plumage as such a landmark is more logical than using the highly variable molt that replaces it. First, juvenal plumage is shared by all birds and is more likely to be homologous across species than the molt by which some juvenal plumage is replaced. Second, juvenal plumage can intuitively be considered a bird's first basic plumage: it is defined as "the first covering of 'true' ('vaned' or 'pennaceous') feathers" (Palmer 1972:72) and includes a bird's first remiges. Third, it is always attained by a complete molt, completeness (or near-completeness) being a unifying characteristic of definitive prebasic molts recognized by the H-P system. For these reasons, Howell and Corben (2000b) recommended that juvenal plumage can be considered a bird's first basic plumage. Thus, a fixed point, presumed homologous in all birds, marks the start of the first plumage cycle. 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.

When juvenal and first basic plumages are considered equivalent, then conventional second basic plumage for all species with alternate plumages is still termed second basic. In SBS species, however, the conventional first basic plumage needs to be renamed second basic plumage, the second renamed third, 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,

something that conventional H-P nomenclature fails to achieve (Fig. 1A versus 1B).

RECOGNIZING UNDERLYING MOLT STRATEGIES

Palmer (1972:74) stated "The great variation in modes of living that have evolved in birds includes such great variation in the nature, timing, etc., of molts and resultant feather generations . . . as to appear to mask any underlying pattern." Similarly, Jenni and Winkler (1994:8) concluded that "in non-passerines the variation in moult and plumage cycles is so diverse that a convincing common nomenclature is quite impossible." Our cumulative experience in observing, investigating, describing, and documenting molt strategies for over 2000 diverse species, from temperate to tropical zones, and in both Northern and Southern Hemispheres, leads us to conclude, however, that an underlying order is present (which, indeed, it should be, assuming that modern birds share a common ancestor).

Once a consistent, fixed point from which to start a nomenclature of molts and plumages is established (i.e., the synonymy of juvenal and first basic plumage), one can recognize consistent patterns of plumage succession, regardless of how the molts and plumages are named. We propose that four underlying strategies of post-juvenal feather replacement can be identified, starting with, and building upon, the Simple Basic Strategy. These four strategies reflect life-history traits to varying degrees, show patterns of phylogenetic concordance (Table 1), and encompass all known patterns of plumage succession. In order of increasing complexity, we term these strategies the Simple Basic Strategy (SBS), the Complex Basic Strategy (CBS), the Simple Alternate Strategy (SAS), and the Complex Alternate Strategy (CAS; Fig. 2). In the first two strategies, adults lack an alternate plumage, while in the last two strategies adults have an alternate plumage. After the first cycle, molts follow a stereotyped pattern that we term the definitive molt cycle (even though plumage may not yet have attained a definitive appearance).

The Simple Basic Strategy (SBS). This is the simplest possible molt strategy and consists of a single basic plumage per cycle, as defined above (Fig. 2). This pattern of plumage succession is relatively uncommon (Table 1), being found primarily in ratites, in some large, long-lived seabirds (e.g., Sphenisciformes, Procellariiformes) that nest on islands traditionally free from predators, and in larger Falconiformes 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 the second prebasic molt typically commences earlier than that of breeding adults.

The Complex Basic Strategy (CBS). This strategy applies to species in which a single molt (traditionally termed first prebasic) or (rarely) two molts are added into the first cycle but no homologous molt(s) occur in subsequent cycles (Fig. 2; it was termed the Modified Basic Strategy by Howell and Corben 2000b). The novel first-cycle molts replace whatever feathers presumably need to be replaced for a bird to survive its first year and enter into the definitive cycle. A plumage similar in appearance to definitive basic plumage usually results, but we consider this similarity analogous, not homologous (see above).

The Complex Basic Strategy is found in a fairly diverse group of birds (Table 1). One reason for its frequent occurrence may be that juvenal plumage grows during the breeding season, while definitive prebasic molts generally follow the breeding season. Consequently, the first cycle is usually slightly longer than definitive cycles, and juvenal plumage would have to be at least as durable as definitive basic plumage if it were to survive the first cycle. But juvenal head and body plumage, at least, is generally poorer than subsequent basic plumages (Jenni and Winkler 1994). 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, novel molt (not repeated in subsequent cycles) by which they attain stronger feathers that protect them until the start of the second prebasic molt.

In most CBS species the inserted first-cycle molt involves only head and body feathers, but in some species it can be complete or nearly so, thus appearing similar to a definitive prebasic molt. Close inspection usually reveals some differences, however: in the added first-cycle molt, birds are more likely to retain a few remiges,

TABLE 1. Molt strategies of North American and Australian birds by family or subfamily. Taxonomy follows AOU (1998) for overall sequence and North American families, Christidis and Boles (1994) for Australian nonpasserines, Schodde and Mason (1999) for Australian passerines, with families integrated by reference to Gill (1994). Numbers in parentheses indicate total number of species considered, followed by number of species for which adequate data exist to assign them to a strategy. × = predominant molt strategy (or strategies) within a family (>35% of species); + = less-frequent molt strategy (<35% of species). ? = this molt strategy may occur, as reported in the literature or suspected by us.

	Simple Basic Strategy	Complex Basic Strategy	Simple Alternate Strategy	Complex Alternate Strategy
Casuariidae (2,1)	×			
Gaviidae (5,3)			×	
Podicipedidae (11,7)				×
Spheniscidae (12,12)	×			
Diomedeidae (12,8)	×			
Procellariidae (50,13)	×	?		
Hydrobatidae (11,2)	×			
Phaethontidae (3,0)		?		
Sulidae (8,5)	×			
Pelecanidae (3,0)			?	?
Phalacrocoracidae (13,5)	?		×	
Anhingidae (2,0)		?	?	
Fregatidae (4,0)	?	?		
Ardeidae (26,7)		+	×	?
Threskiornithidae (7,2)		×	×	?
Ciconiidae (2,0)	?			
Cathartidae (3,3)	×			
Phoenicopteridae (1,0)		?	?	
Anseranatidae (1,1)		×		
Anatidae				
Dendrocygninae (4,2)		×		
Anserinae (11,10)		×	?	
Anatinae (50,22)		?	×	×
Accipitridae (38,30)	×	+		
Falconidae (11,10)	×	+		
Cracidae (1,1)		×		
Megapodiidae (3,3)		×		
Phasianidae (20,8)		×		×
Odontophoridae (6,6)		×		+
Rallidae (25,11)		×	?	×
Aramidae (1,0)		?	?	
Gruidae (4,0)	?	?		
Otididae (1,1)		×		
Turnicidae (6,5)		×		×
Pedionomidae (1,1)		×		
Scolopacidae (60,51)		?	+	×
Rostratulidae (1,1)		×		
Jacanidae (3,1)		×		?
Chionididae (1,1)	×			
Burhinidae (2,1)		×		?
Haematopodidae (5,1)		?	?	×
Recurvirostridae (5,2)		?	?	×
Charadriidae (24,13)		+	?	×
Glareolidae (2,2)				×
Laridae (58,44)	+		×	×
Alcidae (21,6)		?	×	×
"Near-Passerines"				
Columbidae (37,33)		×		?
Cacatuidae (14,6)		×		
Psittacidae (39,25)		×		
Cuculidae (19,19)		×		
Centropidae (1,1)				×
Tytonidae (5,5)	×			
Strigidae (24,22)		×		?
Podargidae (3,3)		×		
Aegothelidae (1,1)		×		

TABLE 1. Continued.

	Simple Basic Strategy	Complex Basic Strategy	Simple Alternate Strategy	Complex Alternate Strategy
Caprimulgidae (12,11)		×		+
Apodidae (8,3)	?	×		
Trochilidae (16,16)		×		
Trogonidae (2,2)		×		
Alcedinidae (13,9)	+	×		
Meropidae (1,1)		×		
Coraciidae (1,1)		×		
Picidae (22,22)		×		
Passerines				
Pittidae (4,3)		×		
Tyrannidae (35,29)		×		×
Menuridae (2,1)		×		
Atrichornithidae (2,1)		×		
Climacteridae (6,6)		×		
Maluridae (22,21)		×		×
Pardalotidae (4,4)		×		
Acanthizidae (45,44)		×		
Meliphagidae (72,66)		×		+
Petroicidae (20,20)		×		
Orthonychidae (2,2)		×		
Pomatostomidae (4,4)		×		
Laniidae (2,1)		?		×
Vireonidae (14,10)		×		×
Eupetidae (8,8)		×		
Neosittidae (1,1)		×		
Pachycephalidae (14,14)		×		
Dicruridae (19,16)		×		
Paradisaeidae (4,4)		×		
Artamidae (14,7)		×		
Campephagidae (8,7)		×		+
Oriolidae (3,3)		×		
Corvidae (23,23)		×		
Corcoracidae (2,1)		×		
Ptilonorhynchidae (10,1)		×		
Alaudidae (3,2)		×		
Dicaeidae (1,1)		×		
Hirundinidae (13,9)		×		+
Paridae (11,11)		×		
Remizidae (1,1)		×		
Aegithalidae (1,1)		×		
Sittidae (4,4)		×		×
Certhiidae (1,1)		×		
Troglodytidae (9,9)		×		+
Cinclidae (1,1)		×		
Regulidae (2,2)		×		?
Zosteropidae (7,1)				×
Sylviidae (14,8)		?		×
Turdidae (20,16)		×		+
Timaliidae (1,1)		×		
Mimidae (10,9)		×		?
Sturnidae (4,1)		×		
Motacillidae (9,9)				×
Bombycillidae (2,2)		×		
Ptilogonatidae (1,1)		×		
Peucedramidae (1,1)		×		?
Parulidae (53,45)		×		×
Thraupidae (5,5)		×		×
Emberizidae (49,47)		×		×
Cardinalidae (10,10)		×		×
Icteridae (22,13)		×		×
Fringillidae (19,18)		×		×
Passeridae (22,5)		×		

rectrices, or primary coverts (e.g., Galliformes, Trochilidae, Timaliidae). Also, comparisons within species or among related species often reveal differences. For example, in the parrot genus *Neophema* and the grosbeak genus *Cardinalis*, the conventional first prebasic molt includes none, some, or all flight feathers (Pyle 1997b, Higgins 1999). In such cases it is apparent that complete postjuvenal molts represent variation within an inserted molt rather than being prebasic molts. We regard the usual occurrence of phenotypic differences between added first-cycle molts and definitive prebasic molts as evidence that these molts have different origins, and are likely not homologous. But in cases where no differences are readily apparent and there are no close relatives from which patterns can be inferred, how can one be sure that the complete postjuvenal molt is not actually a prebasic molt? Following our definition of the first cycle, complete postjuvenal molts are not prebasic if they do not correspond to molts in the Simple Basic Strategy. That is, these birds would gain an extra "basic" plumage relative to the SBS (also see Howell and Corben 2000b).

Species with complete or near-complete inserted first-cycle molts (Pyle 1997a, Flannery and Gardali 2000) usually appear to have good reason to replace flight feathers, given their life-history traits, as these feathers could become too worn to function adequately by the end of their first breeding season, when the next molt occurs. Some are highly aerial and long-distance migrants (e.g., Trochilidae, Hirundinidae), some live in highly abrasive environments (e.g., Wrentit [*Chamaea fasciata*]), and some are cavity nesters that abrade their remiges when entering and leaving the nest (e.g., Picidae, European Starling [*Sturnus vulgaris*]).

The Simple Alternate Strategy (SAS). This strategy applies to species in which at most only a single plumage (traditionally termed first basic and sometimes interpreted as comprising two plumages) is added into the first cycle, and one plumage is added into definitive cycles (Fig. 2). The inserted first-cycle molt usually appears homologous with the prealternate molt of definitive cycles. This strategy is relatively uncommon (Table 1), and was not identified until Howell and Corben (2000a) recognized it in the Western Gull, although over one hundred years ago Dwight (1901) noted this possibility for large gulls. The Simple Alternate Strategy has been documented for several species, for example, White Ibis (*Eudocimus albus*; Beebe 1914, Kushlan and Bildstein 1992) and scoters (Dwight 1914; see Case Studies, below), but it has been difficult to accept, or to identify as such, because H-P convention considers the postjuvenal molt as a first prebasic molt.

The Simple Alternate Strategy has been found mainly in relatively large, aquatic nonpasserines that, as a rule, do not breed in their first year, but critical study is needed to determine how widespread it is. Recently, Snyder and Russell (2002) described the Carolina Parakeet (*Conuropsis carolinensis*) as an SAS species. As with the Complex Basic Strategy, the added first-cycle molt presumably helps a bird survive to the definitive cycle, and it can be quite variable in extent, even within a species (e.g., Howell et al. 1999, Howell 2001a). In some groups (e.g., certain ducks and large gulls), we suspect the SAS came about through loss of a second first-cycle molt (i.e., derived from the Complex Alternate Strategy, following). Preliminary analysis suggests that birds exhibiting SAS include Gaviiformes, Phalacrocoracidae (in which there may be no added first-cycle molt), some ducks (Anatidae), and some large gulls.

The Complex Alternate Strategy (CAS). This strategy applies to species in which two (rarely three) plumages are added into the first cycle, while one (rarely two) added plumages occur in definitive cycles (Fig. 2): for example, many Anatinae and Charadriiformes, and apparently all Passeriformes that have alternate plumages as adults (Table 1). One (rarely two) first-cycle molts (including conventional first prebasic) lack a counterpart in the definitive cycle and function like the novel first-cycle molt of CBS species. Rarely, the novel inserted molts can be complete and appear similar to a definitive prebasic molt, (e.g., Cassin's Sparrow [*Aimophila cassinii*]; Willoughby 1986); see under Complex Basic Strategy for discussion of this situation.

Identifying the homology of inserted first-cycle molts in CAS species can be problematic. Conventionally the second inserted plumage has been termed first alternate, but this may be in large part because the first was, inappropriately, termed first basic. In some cases a review of molt strategies within related families or within an order may suggest a logical pathway for the evolution of added plumages. In theory, a Complex Alternate Strategy could derive from either

the CBS or the SAS. In the former case, definitive alternate plumage and the second inserted first-cycle plumage appear homologous, as with passerines (see Case Studies, below). In the latter case, however, the second inserted first-cycle plumage could equally be the novel plumage, although we have found no case where the evolution of this sequence is suggested. To the contrary, SAS may have derived from CAS in some cases (see Simple Alternate Strategy, above).

IDENTIFYING AND NAMING FIRST-CYCLE MOLTS AND PLUMAGES

From the preceding synopsis of underlying molt strategies, it is apparent that the first cycle can include one, two, or, rarely, three added plumages. We suggest it is most parsimonious to consider molts and plumages present in definitive cycles to have homologous counterparts in the first cycle, unless good evidence exists to the contrary. Thus in species following the Simple Alternate and Complex Alternate Strategies, first-cycle plumages can be identified that appear homologous with definitive alternate plumages (see Case Studies). Still, because the majority of species exhibit Complex Basic or Complex Alternate Strategies (Table 1) they have at least one first-cycle plumage that is not homologous with plumages in the definitive cycle.

What should these unrepeated plumages be called? The H-P system introduced the terms alternate and supplemental for plumages that can be added into a basic cycle. An alternate plumage, attained by a prealternate molt, is any plumage inserted into the basic cycle. Any second plumage (i.e., additional to alternate) added into a basic cycle is termed a supplemental plumage, attained by a presupplemental molt, and it may precede or follow the alternate plumage. These definitions have in general proved to be unambiguous, practical, and helpful in studies of definitive cycles. Naming first-cycle molts and plumages, however, has often proved problematic (as noted above), perhaps because the definitions of alternate and supplemental were proposed with definitive cycles in mind.

Use of the term alternate could, in theory, be appropriate for the unique first-cycle plumage of CBS species with a single inserted molt in the first cycle. However, alternate is not available for use in the same context with CAS species because they already have an alternate plumage in the first cycle; following existing H-P terminology, the unique plumage of CAS species would have to be renamed supplemental. This would lead to contradictions and inconsistencies. For example, treating the unique first-cycle plumage of CBS species as alternate would wrongly imply homology with definitive alternate plumages of closely related CAS species. Alternatively, treating the unique first-cycle plumage of CAS species as supplemental could wrongly imply homology with definitive supplemental plumages (Fig. 4); it would also imply that first-cycle molts homologous to those of CAS species do not occur in CBS species (the unique first-cycle molt of CBS species cannot be called supplemental because there are only two plumages in the first cycle). These problems cannot be dismissed simply as the sort of contradictions that will arise if homologies are sought between birds that are not closely related. In groups such as the vireos (Vireonidae: *Vireo*) and wood-warblers (Parulidae: *Dendroica*) of North America, or the honeyeaters (Meliphagidae: *Certhionyx*) and grasswrens (Maluridae: *Amytornis*) of Australia, some species have definitive alternate plumages while congeners do not (Pyle 1997b, Higgins et al. 2001).

We believe a logical solution to these problems is to introduce a new term to describe plumages unique to the first cycle. Humphrey and Parkes (1959:17) themselves acknowledged that some "cases may well show that parts of our fundamental thesis need to be altered or broadened," and we believe this is such a case. In addition to solving nomenclatural problems, it makes inherent sense that birds could have plumages specifically evolved for the first cycle (as noted earlier). Unique postjuvenal molts and plumages (i.e., ones that lack counterparts in subsequent cycles) have been identified recently for a variety of species (Rohwer 1986, Thompson and Leu 1994), and we are simply extending this concept to another predefinitive plumage.

We propose that the novel, first-cycle plumage conventionally known as first basic plumage in CBS and CAS species can be termed *formative plumage* attained by a *preformative molt.* Because it is a unique plumage, like juvenal plumage, it does not need to be numbered for the cycle in which it occurs (by definition a formative plumage occurs only in the first cycle) although in plumage formulae the use of a suffix "1" can be helpful (as in formative 1, or F1). In addition to the conventional first basic plum-

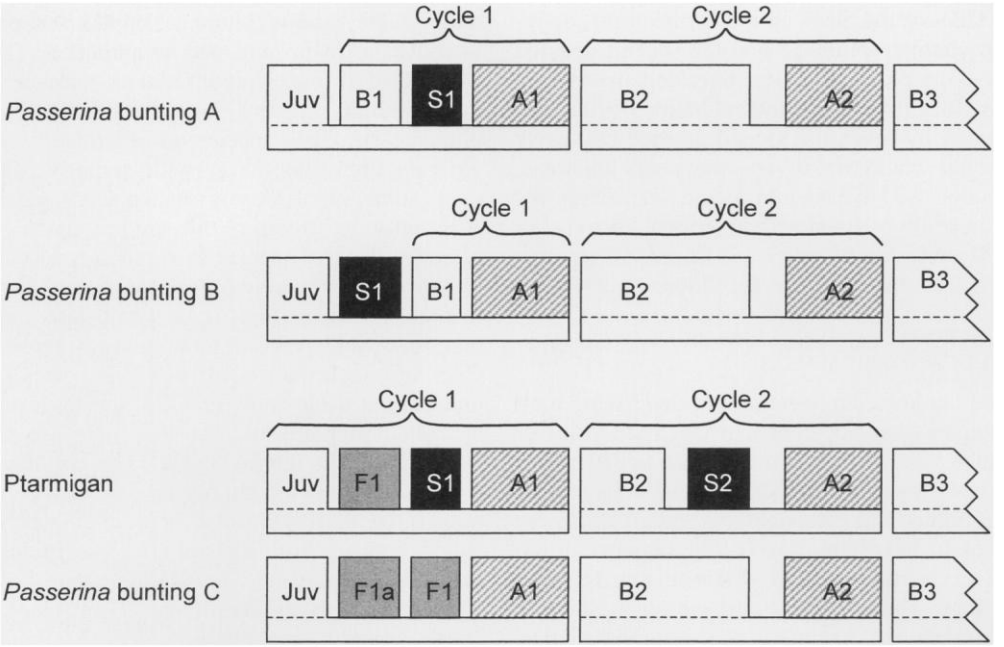


FIGURE 4. Contrast of "first supplemental (S1)" plumage in *Passerina* buntings A (Rohwer 1986), and B (Thompson and Leu 1994) and ptarmigans; and our proposed revision of first-cycle plumage terminology for the same buntings (C). Convention and abbreviations follow Figure 2. By terming novel first-cycle plumages as formative plumages, ambiguity is removed concerning the use of S1: in ptarmigan, S1 is homologous with supplemental plumage in subsequent cycles; in buntings it has been used for a novel, first-cycle plumage.

age of CBS and CAS species, we suggest that the so-called supplemental plumages identified by Rohwer (1986) and others can be viewed as auxiliary formative plumages (see Case Studies). We also hope that recognition of preformative molts and their inherent variability addresses problems raised by Willoughby (1986, 1992). We thus define a formative plumage as any nonbasic plumage present in the first cycle but not in subsequent cycles.

In the event that a species has more than one formative plumage, F1 can be used for the plumage presumed homologous with the single formative plumage (F1) of related species, while F1a, F1b, etc., can be used for auxiliary formative plumages, which may precede or follow F1. For example, if the second described formative plumage in Indigo Buntings (*Passerina cyanea*) appeared homologous to the single formative plumage of other Cardinalidae, then the sequentially first, and novel, formative plumage would be termed F1a (Fig. 4).

We close this section with a practical caution for workers looking to identify between-species homologies for formative (or any nonbasic) plumages. Whereas juvenal and basic plumages can reasonably be presumed homologous across species (Fig. 1B and Fig. 2), nonbasic plumages (i.e., alternate, supplemental, and formative) need not be homologous among species, although usually they are so among closely related taxa. This is an inevitable consequence of different evolutionary histories: for example, alternate plumages have undoubtedly evolved independently among different groups of birds, as acknowledged by Humphrey and Parkes (1959). In studies of molt and plumage succession among different taxa, one should therefore be aware of a potential distinction between homologies of nonbasic plumages *within* a species compared to homologies *between* species.

CASE STUDIES

Applying our revision of the H-P system to all birds is beyond the scope of this paper. Indeed, a literature review indicates that critical data are lacking for some species of nonpasserines (especially in their first cycle) and that data are sometimes contradictory between sources. Inherent problems are that one can seldom follow

individual wild birds over time, and that molt strategies (especially SAS) can be difficult to establish from specimens. Consequently our review should be considered provisional, and it is no more accurate than the data we summarize. We review North American and Australian species because: (1) reasonable data exist for most species; (2) they encompass both Northern and Southern Hemispheres; (3) they include a great diversity of taxa, both resident and migratory; and (4) they include both tropical and temperate species. Thus they should incorporate a wide range of possible molt strategies.

The primary sources for our syntheses of molt strategies in Table 1 were data in regional handbooks for North America (Palmer 1962, 1976a, 1976b, 1988a, 1988b, Pyle 1997b, Poole and Gill 1992–2002), the Western Palearctic (Cramp and Simmons 1977, 1980, 1983, Cramp 1985), and the Australian–Antarctic region (Marchant and Higgins 1990, 1993, Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, unpubl. data). Although these sources used differing systems for naming molts and plumages, enough data were usually provided to allow molt strategies to be determined, at least provisionally. The examples given here align plumage cycles among diverse groups of birds (Fig. 3), although many examples underscore the need for more data. Table 1 discusses taxonomic sequence for families; for orders we follow AOU (1998).

ARDEIDAE

Information for several species, such as Black-crowned Night-Heron (*Nycticorax nycticorax*; Davis 1993, Howell and Pyle, unpubl. data) and Cattle Egret (*Bubulcus ibis*; Cramp and Simmons 1977, Marchant and Higgins 1990) indicates that only a single added first-cycle molt occurs over a bird's first winter, followed by a complete or nearly complete prebasic molt in summer and fall (Fig. 3). Humphrey and Parkes (1963) discussed confusion surrounding the molts of *Ardea herodias* and *A. cinerea*, and we suggest that the data they summarized more reasonably accord with a Simple Alternate Strategy or Complex Basic Strategy than with two putative molts (i.e., conventional first prebasic and first prealternate). Late-molting birds could attain more advanced-looking plumage, as occurs in large gulls (Howell 2001a), but only a single, potentially protracted, and variably extensive molt occurs in the first cycle of any individual bird. Thus, the existence of Complex Alternate Strategy in herons requires substantiation (Table 1).

ANATIDAE

The downy plumage phase of waterfowl is followed by juvenal plumage, and subsequent molts vary considerably in extent and timing both among and within species (Palmer 1976a, 1976b). Members of the subfamily Anserinae (swans and geese) are usually considered to have only a single plumage per definitive cycle (e.g., Palmer 1976a). Juvenal plumage of Anserinae is partially replaced in fall and winter via a variably extensive and often protracted preformative molt; a complete prebasic molt then occurs in summer, after which molts are aligned with the definitive cycle (i.e., CBS; Fig. 3). For some geese, Cramp and Simmons (1977) reported a prealternate molt of head and neck feathers in adults, but we suspect they based their interpretation on seasonal criteria for naming so-called different molts when only a single, almost year-round prebasic molt presumably occurs (Gates et al. 1993).

In Anatini and Aythyini, juvenal plumage is succeeded by formative plumage which, in many species, is very limited in extent and part of a more-or-less continuous transition into the next molt, which produces the bright plumage usually termed alternate (Palmer 1972, 1976a), e.g., Mallard (*Anas platyrhynchos*; Fig. 3). In Mergini, most species appear to retain most to all juvenal plumage well into winter (Palmer 1976b; PP, unpubl. data). Such a strategy, and the description of the timing and extent of two reported molts in the first cycle (Palmer 1976b), recalls the confusion regarding two putative molts in large gulls and herons, when in fact only a single molt may occur. Dwight (1914) described molt in scoters (*Melanitta*) as SAS but was unable to recognize it as such because of confusion derived from traditional terminology, for example, trying to distinguish arbitrary "postjuvenal" and "first prenuptial" molts (within a single, protracted molt) by reference to season or color. Combined field and museum studies of Surf Scoter (*M. perspicillata*; Howell and Corben, unpubl. data) support this interpretation (*contra* Palmer 1976b); thus, at least some Mergini exhibit the Simple Alternate Strategy (Fig. 3).

GALLIFORMES

The molts of North American grouse (Tetraoninae) and quail (Odontophoridae) were detailed by Dwight (1900), and those of Wild Turkey (*Meleagris gallopavo*) by Leopold (1943): two inserted first-cycle molts reportedly occur in all species, although subsequent data do not support this for some quail (Raitt 1961). The prealternate molt of adult gamebirds is limited in most species (ptarmigan being a notable exception) and may not always occur, at least in females. In most species only the preformative molt is extensive, the second inserted first-cycle molt being limited in extent and apparently homologous with the definitive prealternate molt. In turkeys and ptarmigan, however, both the preformative and first prealternate molts are extensive. Two extensive molts in ptarmigan parallel seasonal color change in the adult, while for turkeys Leopold (1943) proposed that these molts were occasioned by the great increase in size during a bird's first year of growth, and thus enable first-year birds to catch up to the definitive cycle.

CHARADRIIFORMES

Considerable data are available for many species (Cramp and Simmons 1983, Cramp 1985, Marchant and Higgins 1993, Higgins and Davies 1996), and this cosmopolitan order includes species that exhibit all four molt strategies. The only species in this order for which the Simple Basic Strategy has been reported are the Chionidae (Marchant and Higgins 1993) and Ivory Gull (*Pagophila eburnea*; Howell 2001b; Fig. 3). The Complex Basic Strategy occurs in the Rostratulidae and, apparently, some Jacanidae, among others (Marchant and Higgins 1993). Data on Charadriidae are equivocal but the family may include species with the Simple Alternate Strategy (*Pluvialis*; Howell and Pyle 2002), Complex Alternate Strategy (most *Charadrius*), and CBS (Marchant and Higgins 1993). Most Scolopacidae and small gulls (e.g., Bonaparte's Gull [*L. philadelphia*]) exhibit CAS, while most large gulls exhibit SAS (Higgins and Davies 1996, Howell 2001a; Fig. 3). As in ducks and passerines, the second added body plumage of the first cycle in sandpipers and small gulls appears homologous with definitive alternate plumage. The cosmopolitan Charadriiformes pose many interesting questions (e.g., where does homology lie in first-cycle molts of remiges?) and could provide worthwhile subjects for examining the evolution of molt strategies in resident and migratory species.

"NEAR-PASSERINES"

Almost all North American and Australian near-passerines (sensu Pyle 1995, 1997b; see Table 1) exhibit the Complex Basic Strategy, while a handful exhibit the Simple Basic Strategy (notably Tytonidae; Fig. 3) and Complex Alternate Strategy. Cramp (1985) considered the juvenal plumage of Tytonidae to be highly reduced and modified to a downy plumage. This is contrary to the generally accepted definition of juvenal plumage (i.e., the first pennaceous plumage in which birds fledge) and we agree with Higgins (1999) that Tytonidae have two downs followed by a durable juvenal plumage. When present, the preformative molt of near-passerines varies from partial (e.g., Strigidae; Pyle 1997c; Fig. 3) to complete (most Columbidae and Trochilidae; Pyle 1995). A second added molt occurs in the first cycle of some hummingbirds, with limited replacement of gorget feathers (Pyle et al. 1997); we consider this an auxiliary preformative molt (Fig. 3).

PASSERINES

Relatively good data exist for the timing and extent of molts in most North American passerines (Pyle 1997b and references therein; Table 1). *Passerina* buntings in particular have been the subject of several recent studies that used the term supplemental for a unique, first-cycle plumage (Rohwer 1986, Thompson 1991, Young 1991). They exemplify the difficulties of identifying homologies by using the conventional H-P system: Thompson and Leu (1994) considered the first postjuvenal plumage of *Passerina* buntings as a first supplemental plumage, followed by conventional first basic, the opposite of Rowher et al. (1992). This involves a novel concept in molt terminology since, by H-P convention, Thompson and Leu's (1994) supplemental plumage occurs *before* the start of the first plumage cycle (Fig. 4). In identifying these plumages, Rohwer et al. (1992) and Thompson and Leu (1994) relied heavily on comparisons with the definitive prebasic molts of *Passerina*. While this approach will produce an answer (one of the first two molts will be more like definitive prebasic than the other) it was based on the premise, which we reject, that one of these first two molts had to be first prebasic. We consider in-

stead that the first cycle of some *Passerina* buntings simply involves two formative plumages (Fig. 4). One still has the problem of determining which of these formative plumages is homologous with the single formative plumage of related species. We suggest to solve this question one should compare the timing and extent of *Passerina* molts with the single preformative molts of related species, and not with definitive prebasic molts.

The only strategies known in North American and Australian Passeriformes are the Complex Basic Strategy and Complex Alternate Strategy (Table 1). The more primitive families mostly exhibit CBS, although partial prealternate molts occur in some species (Table 1, Fig. 3). This suggests that the passerine ancestor had this molt strategy, and it seems reasonable to presume that the second added first-cycle plumage of passerines with CAS is homologous with definitive alternate plumage, as both appear to have been inserted into the CBS.

CONCLUSIONS

Other workers have described the goal of the H-P system as being "to address questions regarding the evolution of molt and plumage sequences in birds" and have advocated that "the H-P system is the *only* existing method suitable for studying the evolution of molt and plumage succession" (Thompson and Leu 1994:778–779). We agree but have found some current use of the conventional H-P system to be arbitrary and thus inconsistent. In particular, automatically assigning the first postjuvenal molt as the first prebasic molt has hindered the recognition of potential homologies in patterns of molting.

Humphrey and Parkes (1963:503) concluded by asking "that critics provide for us and for other students of plumage succession an improved conceptual and terminological framework within which we may all continue productive research in this promising and important field of ornithology." We suggest that the H-P system can be improved by (1) establishing an unambiguous starting point (juvenal plumage) for molt and plumage nomenclature; (2) defining a consistent first plumage cycle; and (3) recognizing the existence of formative plumages. As a consequence, four underlying molt strategies reveal themselves and serve as a working framework from which to approach the subject of molt and plumage sequence.

The ability to place any species in one of four underlying categories is a powerful tool for comparative studies, not least for the evolution of molt strategies across taxa. For example, the simplest basic and alternate strategies (SBS and SAS, respectively) occur only in nonpasserines (Table 1). When working with species whose molt strategies are unknown one now has four options to consider as starting hypotheses, or two options if it is known whether the species in question has an alternate plumage. The ability to categorize all species by these four strategies can also highlight where potential exceptions occur, thus focusing attention on subjects for critical study. We accept, however, that the revised nomenclature we have outlined, while more streamlined than that previously available, is subject to modification with the acquisition of more data. This, like molt itself, is a function of evolution.

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