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COMMENTARY

Searching for consensus in molt terminology 11 years after Howell et al.'s "first basic problem"

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ABSTRACT

Howell et al. (2003) published an innovative augmentation to terminology proposed by Humphrey and Parkes (1959) that classified bird molt on the basis of perceived evolutionary relationships. Despite apparent universal applicability, Howell et al.'s (2003) proposed terminological changes were met with criticism that cited a failure to verify the evolutionary relationships of molt and an inability to recognize homologous molts even within closely related taxa. Eleven years after Howell et al. (2003), we revisit arguments against a terminological system of molt based on evolutionary relationships, suggest an analytical framework to satisfactorily respond to critics, clarify terminology, and consider how to study molt variation within an evolutionary framework.

Keywords: first basic problem, Howell et al. (2003), molt cycle, molt strategies, molt terminology, phylogenetic analysis

Buscando consenso en la terminología de la muda 11 años después de Howell et al. "la problema del primero basico"

RESUMEN

Howell et al. (2003) publicó una argumentación innovadora para la terminología propuesta por Humphrey y Parkes (1959) que clasificaba la muda de las aves basada en las relaciones evolutivas percibidas. A pesar de la aplicabilidad aparentemente universal, los cambios terminológicos propuestos por Howell et al. (2003) fueron considerados con criticismo aduciendo a una dificultad para verificar las relaciones evolutivas de la muda y una falta de habilidad para reconocer las mudas homólogas incluso adentro de taxones cercanamente relacionados. Once años luego de Howell et al. (2003) revisamos los argumentos en contra de un sistema terminológico de la muda basado en las relaciones evolutivas, sugerimos un marco analítico para responder satisfactoriamente a las críticas, clarificamos la terminología y consideramos como estudiar la variación de la muda adentro de un marco evolutivo.

Palabras clave: análisis filogenético, ciclo de la muda, estrategia de la muda, Howell, la problema del primero basico, terminología de la muda

Terminology for molt, the scheduled replacement of feathers, is unnecessarily redundant, as exemplified by the multitude of terms for the same molt (Figure 1). The abundance of jargon stems from classifying molt in relation to environmental or life-cycle seasonality (e.g., breeding; Wolfe and Pyle 2012). Unfortunately, categorizing molt in relation to breeding or seasonality does not provide a universal system of molt terminology because not all birds breed every year or reside in seasonal environments—a fact championed by ornithologists for more than half a century (Humphrey and Parkes 1959, 1963, Rohwer et al. 1992, Howell et al. 2003, 2004). For example, Humphrey and Parkes (1959:14) noted that naming molts on the basis of "environmental and endocrinal phenomena" is problematic because such phenomena "may be related in different ways in different groups of birds, and . . . these relationships can only be obscured by making the nomenclature of plumages and molts contingent on states of any other cycle or developmental processes."

The problems cited by Humphrey and Parkes (1959) are more than theoretical. For example, Jackson (1915) first suggested that the summer body molt in most male ducks should be aligned with the later complete wing molt and,

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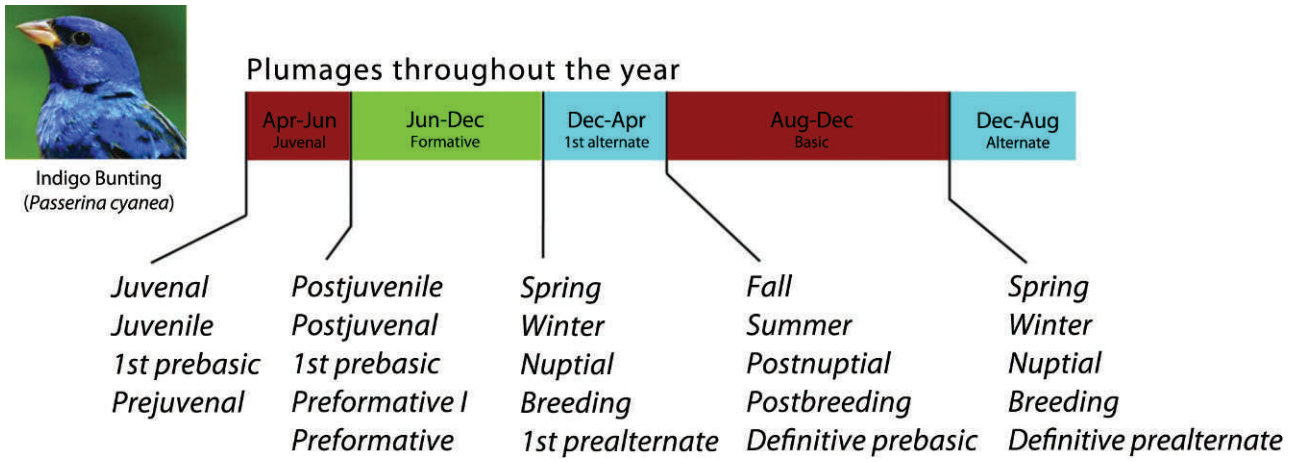


FIGURE 1. Diagram showing the annual plumages of Indigo Bunting (*Passerina cyanea*), following Howell et al.'s (2003) terminology. In addition to plumages, we included examples of redundant molt terminology associated with each plumage.

because it produced a cryptic plumage, Jackson considered this a "winter" plumage followed by a brightly colored "summer" plumage even though it occurs primarily in the winter (Jackson 1915, Pyle 2005). Since Jackson (1915), variations in the terminology for duck plumage and molt have proliferated in the literature, resulting in a diverse, confusing, and sometimes counterintuitive list of molt nomenclature based on season and breeding status (Schiøler 1921, Witherby et al. 1939, Dement'ev and Gladkov 1952, Oberholser 1974, Cramp and Simmons 1977, Marchant and Higgins 1990). The misleadingly descriptive and unstructured nature of such terminology has undoubtedly suppressed or obscured comparative studies in molt and plumage variation across taxa. Humphrey and Parkes (1959), recognizing that classification of molt on the basis of seasonality and life-cycle events unnecessarily differentiates identical molts and ignores the evolutionary history of molt diversification, proposed a unifying system of molt terminology, later augmented by Howell et al. (2003), in which molt terminologies were modified to reflect perceived homologies (Table 1). Importantly, the definition of "homology" used here and by Humphrey and Parkes (1959) refers not to similarity of structure or function, but to historical continuity through inheritance with modification (Wagner 2007). Note that we prefer the term "paralogy" to describe repeated molts within a species because it more accurately reflects their assumed evolutionary relationship, despite the previous use of "homologous" by Howell et al. (2003) in such circumstances, which is instead more appropriate for cross-species comparisons.

The defining difference between Humphrey and Parkes (1959) and Howell et al. (2003) lies in the naming of molt sequences within a bird's first year of life. Humphrey and Parkes (1959) concluded that the prejuvenal molt is unique because it does not have an apparent paralogy later in life. Humphrey and Parkes (1959) also identified the first prebasic molt (i.e. the molt immediately following the prejuvenal molt) as paralogous, with subsequent prebasic molts occurring approximately annually. Because not all species of birds replace all or parts of their juvenal plumage soon after leaving the nest (e.g., many Accipitridae and waterbirds; Howell 2010) and because first prebasic molts can range from being limited to complete across species (Pyle 1997), Howell et al. (2003) modified the terminology of Humphrey and Parkes (1959) by considering the prejuvenal molt synonymous with the first prebasic molt and reclassified the first prebasic molt as a preformative molt that occurs only early in life and lacks paralogous counterparts. As a result, Howell et al.'s (2003) system (hereafter "H-P-H") considers the prebasic molt to be a recurring (often annual) complete or nearly complete paralogous molt, shared by all bird species, that arose deep in evolutionary time; periods between prebasic molts are called "molt cycles." Howell et al.'s (2003) simple changes succinctly aligned molts and plumages across a diversity of taxa, thereby dramatically improving upon the terminological system originally proposed by Humphrey and Parkes (1959; see Howell et al. 2003:figure 1). Howell et al. (2003) further suggested that selective pressures led to the subsequent evolution of other molts inserted between prebasic molts, like the preformative molt, and also prealternate and presupplemental molts, defined by the cycle in which they occur (Table 1). Recognizing the number or type of inserted molt(s) within each cycle places every bird into 1 of 4 "molt strategies" (Howell et al. 2003, Pyle 2008, Howell 2010).

Substantiating H-P-H assumptions is an important step toward more rigorously examining the diversification of feathers and their maintenance through molt that has allowed birds to colonize the Earth's surface. Additionally, understanding the nature of inserted molts would provide

TABLE 1. Important molt and plumage definitions following Pyle (2008) and Howell (2010).

Terminology	Description
Prebasic molt	Prebasic molts occur approximately annually in most birds, are complete to nearly complete, and delineate molt cycles. The first prebasic or prejuvenal molt results in the juvenal plumage. The prejuvenal molt usually occurs soon after hatching and often replaces natal down. Juvenal plumage is the *first* pennaceous coat of feathers. The prejuvenal molt is ubiquitous (occurring in all birds) and is complete in extent (replacing all feathers). Howell et al. (2003) considered the prejuvenal molt comparable with later prebasic molts and, therefore, synonymous with the first prebasic molt.
Preformative molt	Results in the formative plumage. Synonymous with the first prebasic molt of Humphrey and Parkes (1959). The presence and extent of the preformative molt are extremely variable across birds. The preformative molt is unique because it occurs only within the first molt cycle and lacks counterparts in subsequent molt cycles. Sometimes 2 preformative molts occur within the first molt cycle, in which case a second preformative molt is referred to as the ''auxiliary preformative molt.''
Prealternate molt	Results in the alternate plumage. The presence and extent of the pralternate molt are extremely variable across birds. When it occurs, it is often the third molt in the first cycle (in addition to the preformative molt) and the second molt found in each subsequent molt cycle (in addition to the prebasic molt).
Presupplemental molt	Results in the supplemental plumage, which can be the fourth molt in the first molt cycle (in addition to the prejuvenal, preformative, and prealternate molts) and the third molt in subsequent molt cycles (in addition to the prebasic and prealternate molts). If a species has additional presupplemental molts, they are referred to as ''presupplemental a,'' ''presupplemental b,'' etc.
Molt cycle	Period between prebasic molts. For example, birds enter the first molt cycle upon beginning their prejuvenal molt; at the start of the second prebasic molt, they enter the second molt cycle.
Definitive	Here, we suggest that ''definitive'' be used only to describe molts and plumages derived from definitive molt cycles (second or later molt cycle for the majority of species). Definitive molt cycles are defined as having molts with counterparts in subsequent cycles. Thus, first, most cycles that exhibit preformative molts are not considered definitive, because the preformative molt occurs only within the first cycle.

insights into why certain avian lineages were more prone to acquiring extra molts, which may have facilitated life-history evolution. For example, there appear to be correlations between migratory behavior and the presence and extent of inserted molts. These extra molts may have arisen to mitigate structural damage associated with a migratory lifestyle and subsequently commandeered to reflect honest signals associated with winter-ground quality through changes in plumage coloration (Svensson and Hedenström 1999, Pyle and Kayhart 2010, Wolfe and Pyle 2011).

Like other physiological processes and behaviors, molts have presumably resulted from an evolutionary history in which simple adaptations preceded increasingly complex ones. For example, birds molt their feathers at least once a year, so parsimony suggests that an annual molt is a shared characteristic that preceded later inserted molts (which are not shared across taxa) and likely descended from their most recent common ancestor, instead of having evolved multiple times. Although highly variable in timing, this presumably ancestral annual molt is not known to have been lost in any extant birds (although geese may rarely skip an annual molt; see Summers 1983, Summers and Martin 1985), whereas the ability to fly has been lost potentially hundreds of times (Steadman 1989). Given that variation in molt insertions and in the timing of the annual molt probably aided in the global radiation of birds, we believe that a universal terminology encompassing the diversity of molt will promote collaborative study and a deeper understanding of avian evolution.

Here, to move us toward a unified molt terminology, we provide a review of hindrances associated with H-P-H and suggest an analytical framework to address such problems. We also assess ambiguous terminology associated with H-P-H and offer clarifications. Hereafter, to be as consistent as possible, we follow Howell et al.'s (2003) convention for naming molts and plumages (see Table 1).

Problems with H-P-H and Classifying Molt by Evolutionary History

Despite H-P-H's potential to improve our understanding of molt and despite its universal applicability, critics noted the system's many evolutionary assumptions, including presumed and untested homologies across, and paralogous annual molts within, species (Willoughby 2004, Jenni and Winkler 2004). Other critiques of H-P-H suggested that Howell et al. (2003) lacked appreciation for the plasticity of molt, which can obscure homologies (Willoughby 2004, Jenni and Winkler 2004). For example, diversity in the number of molts, extent of each molt, and color of the subsequent plumage can be tremendously variable among closely related taxa such as cardueline finches, making the identification of molt homologies difficult, if not impossible (Willoughby 2004; but see Howell 2010). Additional

problems included difficulties in verifying Howell et al.'s (2003) assumption of paralogy between prejuvenal and later prebasic molts (Willoughby 2004, Jenni and Winkler 2004); even Howell et al. (2003:639) suggested that prejuvenal and prebasic molts "may be analogous based on a widely shared function" rather than resulting from a shared evolutionary history and underlying physiological process. An additional problem associated with H-P-H is variation in the definition of "molt strategy," reflecting an inability to differentiate inserted molts. Howell et al. (2003) first defined different molt strategies by determining which inserted molt occurs within a particular cycle (e.g., prealternate or preformative molt within the first cycle; see Table 1). Pyle (2008) modified the definition of molt strategies by identifying the number of insertions (e.g., 1 or 2 insertions within the first cycle), thereby recognizing an inherent difficulty in distinguishing between first-cycle prealternate and preformative molts in some species (e.g., Ancient Murrelet [*Synthliboramphus antiquus*]; Pyle 2009). Most recently, Howell (2010) seemingly hybridized the 2 approaches by defining molt strategy on the basis of number of insertions, which usually correspond to a particular inserted molt, within a given cycle.

In response to critics, Howell et al. (2004) reiterated that feather color should not be used to identify homologous molts and that molt homology should be considered "comparable," awaiting verification of evolutionary origins when "a genetic basis will eventually be discovered that can reveal homologies of molts" (Howell et al. 2004:207). Although H-P-H may be correct in assuming that an annual molt is highly conserved, note that timing of development is one of the most variable elements of evolution and that the vast majority of morphological evolution occurs through changes in developmental timing (West-Eberhard 2003). We propose that the evolution of molt should be studied under the framework of heterochrony, or changes in timing of developmental events. Developmental events and associated regulatory genes are evolutionarily malleable and easily duplicated, and molt is a physiologically complicated process. Repeated annual molts in birds are likely paralogous, and inserted molts may be the result of duplication and modification of an ancestral molt. On the basis of these realizations, we believe that 2 questions must be addressed to verify H-P-H assumptions and move toward a universally accepted system of molt terminology: (1) What was the ancestral molt? (2) How many times and why have inserted molts arisen?

Testing H-P-H Assumptions

One major obstacle in testing H-P-H assumptions is the determination of whether the prejuvenal and later prebasic molts are paralogous within, and homologous across, taxa. Within species, the relationship between prejuvenal and prebasic molts may represent a synapomorphic character or, conversely, 2 independently derived traits with respect to other molts. Distinguishing between these possibilities is difficult because every known bird species has a molt resembling the prejuvenal and prebasic molt, which limits our ability to analyze variation within a phylogenetic framework. If the prejuvenal and prebasic molts evolved independently deep in evolutionary time, then regulation of prejuvenal and prebasic molts may operate independently and might be assessed through transcriptomic analysis. Such an analysis could sample a diversity of species and molts to assess how dissimilar molts are activated within and across species. Results of a transcriptomic analysis experiment would cluster molts by their expression profile, allowing analysts to determine expression and genetic similarities of molts within an individual. Despite apparent potential for transcriptomic analysis, we realize that molt is likely determined by many genes, gene duplication, or manipulation in the timing of events (Carroll 2008), thereby complicating molecular analysis focused on determining the evolutionary relationship of paralogous molts within a species.

Despite inherent difficulties in examining evolutionary relationships of paralogous molts within species, variation in patterns of the prebasic molt may shed some light on this issue. All birds molt their feathers simultaneously during the prejuvenal molt, and many groups of birds molt remiges simultaneously as adults (e.g., Gaviidae, Rallidae, Anatidae, Alcidae, and Gruidae; Pyle 2008). This retention of a juvenile trait into adulthood may be viewed as an example of neoteny. The fact that simultaneous molt, when exhibited in adults, is expressed during prebasic molts and never during the preformative or prealternate molts provides evidence for ancestral relationship and physiological connection between the prejuvenal and prebasic molts (Pyle 2008). Because parsimony and similarities in feather replacement strongly suggest a shared evolutionary origin of annual molts (prebasic and prejuvenal) within species, the number and extent of inserted molts (preformative, prealternate, and presupplemetal molts; see Table 1) between prebasic molts can be examined as characters throughout a phylogeny to estimate relationships between similar molts in different species, in much the same way that behavior is examined by ethologists (Greene and Burghardt 1978; Figure 2). Testing this assumption would determine whether multiple insertions within molt cycles (e.g., prealternate and preformative molts) in gulls (Laridae) and warblers (Parulidae) are the result of 1 or multiple evolutionary events. Realistically, finding single origins for inserted molts across all bird taxa is not likely and does not render the fundamental concept of H-P-H nomenclature invalid; it would only necessitate

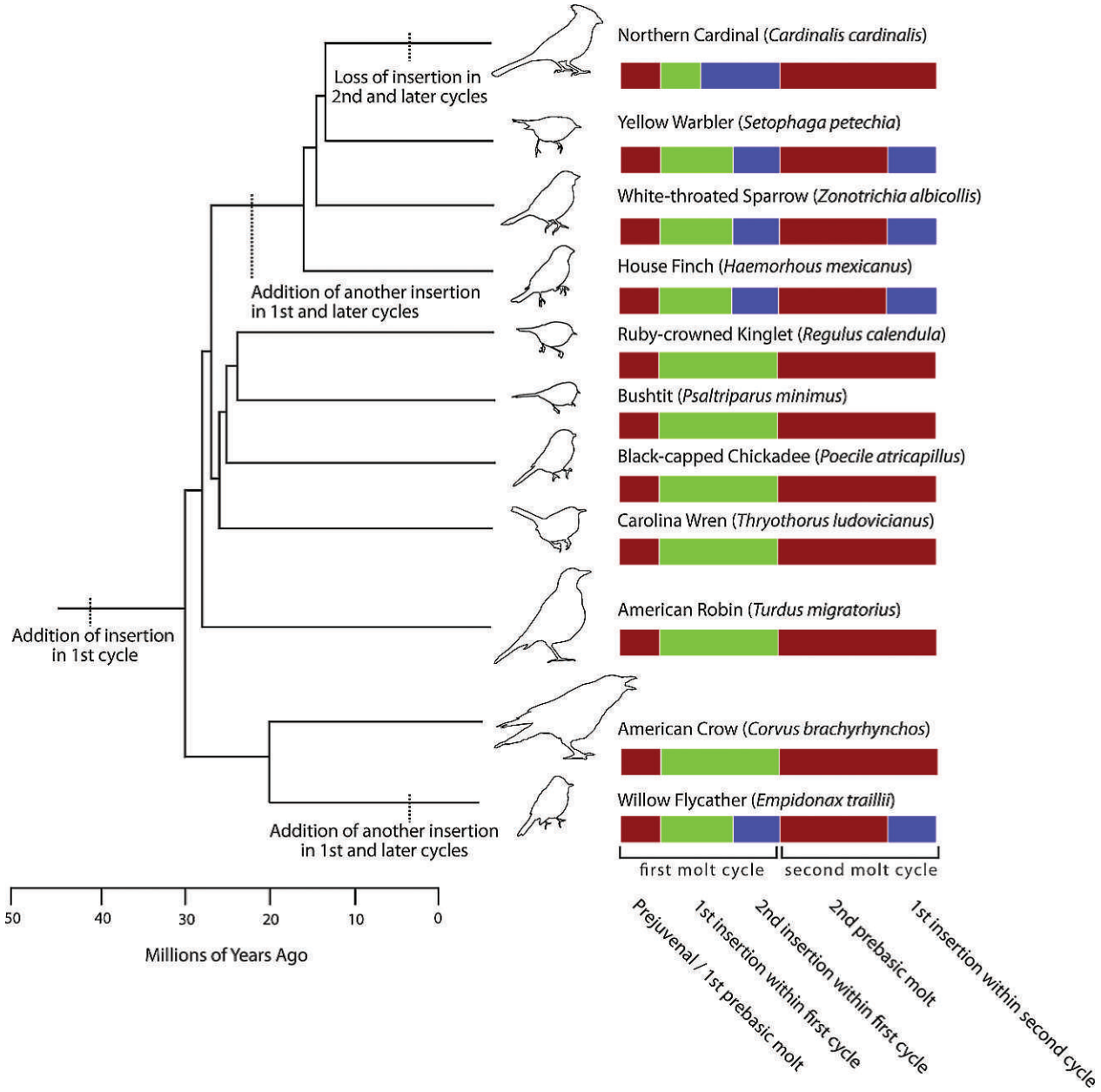


FIGURE 2. Schematic illustrating our proposed analysis whereby molt insertions are associated with individual species, across a phylogeny, to ascertain whether insertions denote synapomorphies across distantly related taxa. Our schematic is based on the phylogeny proposed by Sibley and Ahlquist (1990).

new definitions of inserted preformative, prealternate, and presupplemental molts reflecting their homoplasy.

Clarification of Terms

In addition to testing H-P-H assumptions, ambiguous molt terminology associated with H-P-H must be clarified. In particular, the term "definitive" is used in 4 different contexts: (1) plumage maturation (*definitive plumage*), (2) molts that produce a fully maturated plumage (*definitive molt*), (3) molts that have paralogous counterparts in subsequent cycles (*definitive molt*), and (4) cycles that include only molts with paralogous counterparts in subsequent cycles (*definitive molt cycle*) (Humphrey and Parkes 1959, Rimmer 1988, Heise and Rimmer 2000, Howell et al. 2003, Pyle 2008). Originally, Humphrey and Parkes (1959) suggested the term "definitive" to describe maturated plumages; unfortunately, using "definitive" in its original context is confusing, as exemplified by White-crowned Manakins (*Dixiphia pipra*). In the first cycle, these manakins undergo a partial preformative molt,

resulting in a green bird with some retained juvenal feathers for the remainder of the first cycle. The second prebasic molt is complete in extent, resulting in green males and females without retained juvenal plumage. After the third prebasic molt, females remain green (and are identical to second basic females), but males transition to a striking black and white plumage that is either fully maturated or becomes fully maturated after the fourth prebasic molt (Ryder and Durães 2005). Therefore, despite being the same age, female White-crowned Manakins enter a "definitive plumage" (sensu Humphrey and Parkes 1959) 1 or 2 yr before males, even though a "definitive molt" or "definitive cycle" commences with the second prebasic molt in both sexes. Some other species, such as Wrentit (*Chamaea fasciata*), undergo a complete preformative molt that results in a fully maturated plumage aspect, similar to second and later basic plumages (Pyle 1997). These 2 examples demonstrate that a definitive plumage could result from a definitive preformative, second prebasic, third prebasic, or fourth prebasic molt; thus, the term "definitive" as currently used is context dependent and confuses a discussion of evolutionary relationships across and even within species.

We believe that using "definitive" to describe plumage maturation violates the spirit of H-P-H, in which 1 molt results in 1 plumage and is not used to classify plumage aspect (Howell et al. 2003). Presumably on the basis of this realization, Pyle (2008:13) used molts with paralogous counterparts in subsequent cycles to define definitive molts as attaining "stasis in terms of extent and timing, irrespective of plumage aspect." It may seem natural to define definitive molts as having paralogous counterparts in subsequent cycles (sensu Pyle 2008); however, this definition presents inconsistencies where the prejuvenal molt, presumed to be paralogous with later prebasic molts, might be considered definitive but is followed by a preformative molt that lacks counterparts in subsequent cycles. We suggest that molt and plumage terminology should be consistently applied across taxa to better reflect presumed evolutionary history and, thus, recommend that "definitive" be used only in the context of describing molt cycles and the molts that occur within them, irrespective of plumage aspect. In this context, the second molt cycle would represent the definitive molt cycle in most birds and, therefore, individual molts occurring within the second and later cycles should be considered definitive.

In conclusion, H-P-H is a unique system of nomenclature because, like systematics and taxonomy, it strives to base molt terminology on the evolutionary history of the subject. However, no major attempt has been made to validate the evolutionary framework in which H-P-H classifies molt. To move toward molt nomenclature consensus, the evolutionary assumptions of H-P-H must be tested and the terminology solidified. Through phylogenetic analyses and a stronger understanding of underlying physiological and genetic controls of assumed prebasic molts, researchers will begin to subject the H-P-H system to continual refinement, thereby providing novel insights into avian evolution and natural history.

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