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COMMENTARY

Use of "definitive" and other terms in molt nomenclature: A response to Wolfe et al. (2014)

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ABSTRACT

Ornithologists have largely embraced the molt terminology of Humphrey and Parkes (1959) as modified by Howell et al. (2003; the H-P-H system). In a recent commentary, Wolfe et al. (2014) summarized the derivation and benefits of H-P-H terminology, suggested slight modifications, and promoted analyses on the evolution of molts using H-P-H nomenclature. We appreciate the timeliness of Wolfe et al.'s review and agree with most of their conclusions and modifications. We disagree, however, with Wolfe et al.'s proposal for introducing a new and restricted use of the term "definitive" in H-P-H nomenclature. To avoid confusion, we recommend that definitive plumage and definitive molt cycle continue to be used as defined by Humphrey and Parkes (1959) and Howell et al. (2003), respectively, as terms indicating that plumage appearance and molt cycle have achieved stasis. We also recommend that the term "plumage" can be used more widely than the definition proposed by Humphrey and Parkes (1959), and that the term "juvenal" can henceforth be replaced by "juvenile" in molt and plumage literature.

Keywords: definitive, juvenile, molt cycle, molt strategies, plumage

Uso de "definitivo" y otros términos en la nomenclatura de la muda: Respuesta a Wolfe et al. (2014)

RESUMEN

Los ornitólogos han acogido ampliamente la terminología sobre muda de Humphrey y Parkes (1959) y modificada por Howell et al. (2003; sistema H-P-H). En un comentario reciente, Wolfe et al. (2014) resumieron el origen y los beneficios de la terminología H-P-H, sugirieron modificaciones sutiles, y promovieron los análisis sobre la evolución de la muda usando la nomenclatura H-P-H. Apreciamos la oportuna revisión de Wolfe et al. y estamos de acuerdo con la mayoría de sus conclusiones y modificaciones. Sin embargo, no estamos de acuerdo con la propuesta de Wolfe et al. de introducir un nuevo uso restringido del término "definitivo" en la nomenclatura H-P-H. Para evitar confusión, recomendamos que los términos de "plumaje definitivo" y "ciclo de muda definitivo" sigan siendo usados como fueron definidos por Humphrey y Parkes (1959) y por Howell et al. (2003), respectivamente, como términos basados en la estabilidad que generalmente alcanza el aspecto del plumaje. También recomendamos que el término "plumaje" pueda ser usado más ampliamente que en la definición propuesta por Humphrey y Parkes (1959), y que el término "juvenal" pueda entonces ser reemplazado por "juvenil" en la literatura sobre muda y plumaje.

Palabras clave: ciclo de muda, definitivo, estrategias de muda, juvenil, plumaje

Ornithologists, particularly those in the Americas, have largely embraced the molt terminology of Humphrey and Parkes (1959; the H-P system). This nomenclature divorces molt terms from reproductive and seasonal terms, basing terminology instead on presumed or perceived evolutionary relationships. It thereby allows direct comparison of bird molt strategies throughout the world, in a context independent from variations related to proximal life-history events. The H-P system has largely stood the test of time, with the exception of a simple yet critical modification to terminology within a bird's first cycle (that is, considering a bird's juvenile plumage as its first basic plumage), recommended by Howell et al. (2003). This modified ("H-P-H") terminology has led to a better understanding of molt cycles by ornithologists and students, and has been used to derive an age-coding system for birds that lacks the problems of calendar-based and other systems (Wolfe et al. 2010, Johnson et al. 2011).

In a recent commentary, Wolfe et al. (2014) summarized the derivation and benefits of H-P-H terminology, responded to previous criticisms of it, suggested slight modifications, and promoted analyses using H-P-H nomenclature to investigate the evolution of molts from ancestral to recent bird taxa. We appreciate the timeliness

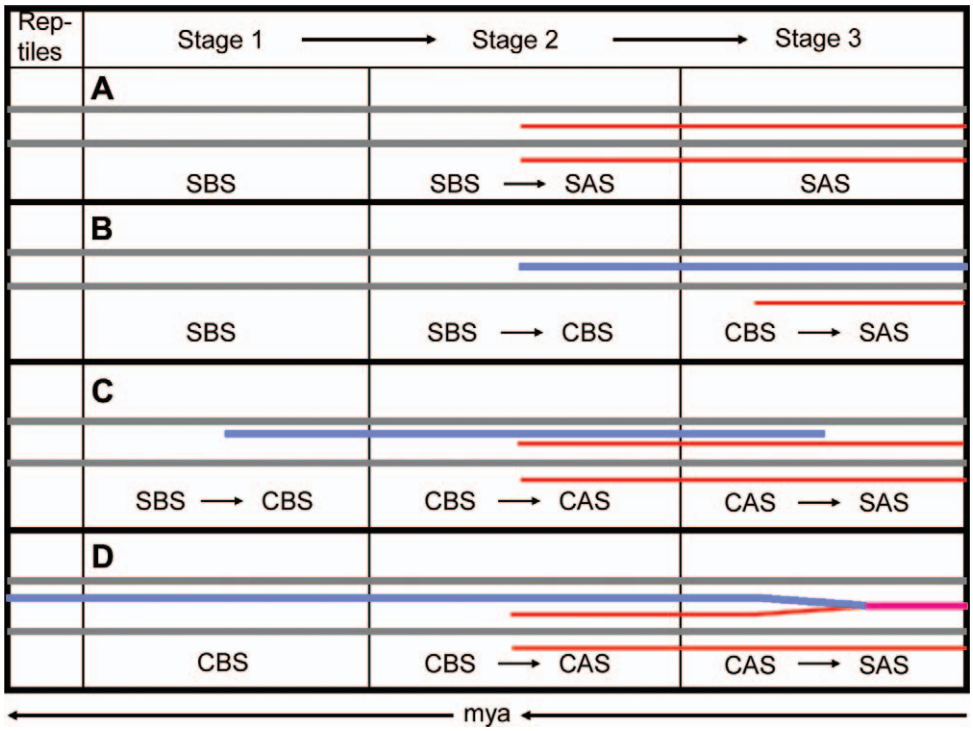

FIGURE 1. Potential evolutionary pathways reflecting addition and loss of inserted molts, from reptiles through ancestral birds, which could result in a Simple Alternate Strategy (SAS) in present-day bird species. For each species (A–D), the upper gray line indicates the first prebasic molt/molt cycle and the lower gray line the definitive prebasic molt/molt cycle; blue lines indicate preformative molts and red lines prealternate molts. (**A**) Addition of prealternate molts in both first and definitive cycles; (**B**) addition of a preformative molt, followed by addition of a prealternate molt in the definitive cycle; (**C**) addition and loss of a preformative molt, followed by gain of prealternate molts in both cycles; (**D**) continuation of the preformative molt from reptiles, addition of prealternate molts in both first and definitive cycles, and merging of preformative and prealternate molts in the first cycle (Pyle 2009).
See Pyle (2013a) for discussion of the possibility that the preformative molt in birds may have evolved from an ancestral ecdysis event present in young reptiles as their body size increases (as in species D), and Howell (2010:33–34) for further discussion of the pathways by which molt strategies in birds might have developed.

of Wolfe et al.'s review and agree with most of their conclusions and modifications. We particularly support their emphasis that the H-P-H framework be based on a species' evolution from ancestral taxa, rather than on proximal factors (also see Figure 1 and Pyle 2005, 2007, 2009, 2013a). We disagree, however, with Wolfe et al.'s (2014) proposal for introducing a new and restricted use of the term "definitive" in H-P-H nomenclature. We explain here the reasons for our stance, and also suggest 2 other ways to streamline H-P-H molt terminology.

Definitive Ambiguity

Humphrey and Parkes (1959) originally used the term "definitive" to indicate a mature plumage "aspect" (see below) and the molts that produce this aspect (e.g., the definitive prebasic molt). Howell et al. (2003) expanded the term definitive to describe molt cycles after the first cycle, in which molts follow a stereotyped pattern, including extent and timing (Pyle 2008), even though plumage may not have attained a definitive aspect. The latter was perhaps a novel published use of definitive (although for some time we had encountered this use in conversation), but its meaning is fairly intuitive given that the H-P system had already introduced the term as a description of something (plumage aspect) that has achieved a kind of stasis. Wolfe et al. (2014) recommend discontinuing the use of the term "definitive" for all of these situations, using it instead "to describe molts and plumages derived from definitive molt cycles," a definitive molt cycle now being that in which the number of molts within a cycle reaches stasis.

Definitive plumage aspect is assumed during the first or second molt cycle in most passerine birds, the third or fourth cycle in most gulls, and later molt cycles in some larger bird species (Pyle 1997, 2008; Howell 2010). As Wolfe et al. (2014) point out, for a variety of reasons this definition of definitive does not promote understanding of molts in an evolutionary context. First, due to substantial

variation in the attainment of definitive appearance, both between closely related species and among age/sex groups within a species, the concept of "definitive plumage aspect," as defined by H-P-H, lacks both homology and parology. For example, in some species of shearwaters the first basic plumage (= juvenile; see below) can be considered definitive, whereas in some albatrosses the definitive plumage aspect can be reached anywhere between the 10th and 20th molt cycles, depending on the individual and sex (Prince et al. 1997, Pyle 2008).

Second, differences between predefinitive and definitive plumage aspects can show essentially continuous variation, from very subtle (involving slight variation in feather shapes only) to very marked (involving complete differences in body-feather coloration), and there is currently no clear point along this continuum to assign the term definitive, within and among individuals and species.

Third, and last, once definitive plumage aspect has been assumed, older individual birds may continue to exhibit variable plumage coloration between cycles, related to interactions of molt with hormonal cycles that affect pigment deposition on growing feathers (Pyle 2008, 2013b; Howell 2010). These problems of equating molts with plumage aspect reinforce the premise that plumage coloration should be divorced from molt-cycle terminology (Howell et al. 2003, 2004; Pyle 2005, 2007, 2013a; Howell 2010).

The restricted definition of Wolfe et al. (2014) results in the second-cycle molts and plumages equating to definitive-cycle molts and plumages in most if not all birds; the exceptions perhaps being those relatively few present-day species exhibiting the Simple Basic and Simple Alternate Strategies, in which the first-cycle molts and plumages would be definitive-cycle molts and plumages following Wolfe et al. (2014). However, because inserted molts may be added or lost over time (e.g., Figure 1), a definitive molt cycle sensu Wolfe et al. (2014) could be different at various times along the ancestral lineage of a species (Figure 1). This possibility negates Wolfe et al.'s (2014) primary stated purpose for changing the definition of definitive "to better reflect presumed evolutionary history."

If we are to adhere to one of Humphrey and Parkes' (1959) original important advancements, that the name of a plumage should follow that of the preceding molt (e.g., a second prebasic molt results in second basic plumage), substantial confusion will occur (if we follow Wolfe et al. 2014) over what to call second-cycle and later plumages that are distinguishable from older plumages. This is because "definitive" second-cycle molts would now produce definitive plumages according to Wolfe et al. (2014) but would not produce definitive plumages sensu H-P. Such confusion would have negative consequences on the age terminology proposed by Wolfe et al. (2010), in which the separation of second-cycle from definitive-cycle molts and plumages is an important part of the age-coding process for many species. In most large gulls, for example, "Definitive Cycle Basic (DCB)" places an individual in a clearly older age group than "Second Cycle Basic (SCB)" yet this distinction would be lost or, at best, confused following the restricted definition of "definitive" according to Wolfe et al. (2014).

We also note that the H-P definition of definitive has gained some following, especially in the Americas (e.g., in Poole 2014). Many ornithologists therefore have preconceptions about the term's meaning, and it will continue to appear in published literature. Failure to recognize this reality could increase rather than diminish ambiguity because, without qualification, readers will be unable to tell which definition a particular writer might be following.

To avoid confusion, *we recommend that "definitive plumage" and "definitive molt cycle" continue to be used as defined by Humphrey and Parkes (1959) and Howell et al. (2003), respectively, as terms indicating that a plumage aspect or molt cycle has generally reached stasis*. These are useful placeholder terms to separate such plumages and molt cycles from those of previous identifiable cycles. It should be understood, however, that the H-P system did not introduce the term "definitive" to reflect any homology or parology, simply as a semantically neutral term for what, in everyday parlance, is called "adult plumage." Had we reviewed a draft of the Wolfe et al. (2014) commentary prior to publication, we might have suggested that they propose a new word for their purposes, rather than attempt to redefine an established term.

Coming to Terms with Plumage and Juvenile

As we indicate above, attempting to redefine definitive at a time when ornithologists and students are still learning the value of H-P-H terminology risks confusion, which in turn may discourage advancement in our collective understanding of bird molts. Such was the case when Humphrey and Parkes (1959) themselves attempted to redefine the term "plumage." Formerly, plumage was simply equated to a bird's feathering, as generally related to structure and appearance, but the H-P system defined the term more narrowly, as "a single generation of feathers" resulting from a specific molt.

The H-P system introduced the term "aspect" to indicate the outward appearance of a bird's feathering, and yet another term, "feather coat," to indicate up to multiple generations of feathers following molts. Differences between these 3 definitions are confusing to most students and researchers of bird molt, such that the terms aspect and feather coat have not gained traction in the ornithological literature; in particular, aspect has been frequently misused and misunderstood (e.g., see Howell 2009). Moreover, the H-P redefinition of plumage has fostered considerable ambiguity and misunderstanding

about molt (and "plumage") homologies (e.g., see Howell et al. 2004, Howell 2010:20–21).

We suggest that the term "plumage" can be used to describe all 3 of these concepts, with the use of modifiers clarifying which shade of meaning is intended. Indeed, "plumage" is still used widely for all 3 concepts by ornithologists (especially outside the Americas), and intended meaning is usually clear from context; whether or not this is desirable it is the reality of the situation. Thus, for example, a first prealternate molt results in first alternate plumage (as intended by the H-P redefinition of "plumage"); it may or may not resemble the breeding plumage (= H-P aspect) of adults; and it may result in 3 generations of feathers in a bird's plumage (= H-P feather coat). One can also say that a bird has bright or red-and-green plumage (= H-P aspect), mixed fresh and worn plumage (= H-P feather coat), or formative plumage (= H-P plumage). We do not believe that meaning is compromised substantially, or ambiguity fostered, by approaching the term plumage with modifiers in this manner.

Similarly, in another admirable attempt at precision, Humphrey and Parkes (1959) restricted the term "juvenal" as an adjective in the sense of juvenal plumage (following Dwight 1900, 1902), and used "juvenile" as a noun referring to a bird in juvenal plumage. Because of perceived confusion, Eisenmann (1965) proposed that juvenal be used for both the plumage and the bird wearing it. Despite the efforts of those well-meaning authors, confusion and misuse of "juvenal" and "juvenile" continue to this day, at least in North America ("juvenal" is not used in the European body of molt literature).

We suggest that occasionally misusing 1 term is preferable to misusing 2, and that, again, context makes the meaning of "juvenile" unambiguous. Thus, for example, juvenile birds wear juvenile plumage, comprising juvenile feathers. Hence, juvenal is best expunged as simply another redundant term that clutters the molt lexicon, confuses students, and thus hinders understanding of this important subject; this move has already been made elsewhere (Howell 2009, 2010) and, as noted above, "juvenile" alone is used outside the Americas, with no apparent loss of communication.

Clarity in terminology is important when discussing any branch of avian biology, and the lack of it has been particularly detrimental to research on molts and plumages, both before and after the H-P system was proposed. However, the redefinition of long-established terms, or the application of needlessly restrictive terms to imply false precision, adds a layer of potential confusion that can hinder, rather than promote, understanding. We believe that the modifications suggested above, in use of the terms "definitive," "plumage," and "juvenile," will improve communication in the study of molts and plumages. Moreover, they adhere to 1 of the 4 fundamental tenets proposed by Humphrey and Parkes (1959:14) for a working molt terminology: "the nomenclature must be consistent and *as simple as possible*" (emphasis ours).

In conclusion, we recommend that "definitive" continue to be used as proposed by Humphrey and Parkes (1959) and by Howell et al. (2003); that the H-P terms "aspect" and "feather coat" are unnecessary—"plumage" can be used for both, with context making meaning clear; and that "juvenal" is another redundant term that can be replaced by "juvenile," again with context obviating any ambiguity.

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