Moult Terminology: Envisioning an Evolutionary Approach

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The study of avian moult has been inhibited not only by its complexity but by convoluted and often conflicting terminologies that have combined to cloud the subject. Over time, two nomenclatures have emerged with differing bases of definition. The 'life-cycle' system is used widely in European literature (e.g., Cramp 1988, Jenni & Winkler 2020) and defines moult terms based on timing relative to current-day life-history events, primarily breeding. Conversely, the Humphrey-Parkes or 'H-P' system (Humphrey & Parkes 1959, as modified by Howell et al. 2003), is used more widely in the New World and Australia (e.g., Higgins & Davies 1996; Pyle 2008, 2022a; Howell 2010), and defines terms based on the principle of how moults have evolved along avian lineages (Pyle 2022b).

Recently, Kiat (2022) proposed that moult terminology be simplified, and advocated use of the life-cycle approach as a more understandable system to those not familiar with moult terminology. We appreciate and endorse Kiat's (2022) plea for a simpler moult terminology, and we empathize with his frustration, but we disagree with his primary conclusion. We argue that if one intends moult to be a subject for study, then a standardized terminology based on the best scientific evidence is preferable to a system that, while perhaps more widely understood among ornithologists and the general public for passerines in boreal regions, is often imprecise or ambiguous and is difficult to apply to the majority of avian taxa on a global basis (Higgins & Davies 1996, Howell et al. 2004, Johnson and Wolfe 2018, Kiat 2022, Pyle 2022b).

The debate over the best moult and plumage terminology to use has persisted since the H-P system was proposed by Humphrey and Parkes (1959) over 60 years ago (e.g., Howell et al. 2003, 2004; Jenni and Winkler 2004, 2020; Kiat 2022; Pyle 2022b; and references therein). At this point, certain opinions on which system should be favoured are calcified, and we do not wish to belabour the details yet again. In our experience, however, newer students grasp the H-P system quickly, whereas older ornithologists—including ourselves—who first learned life-cycle moult terminology, often have initial difficulty envisioning the H-P system's evolutionary approach. Our goal with this perspective is to propose and illustrate how moults may have evolved in birds, with the hope that it will assist future ornithologists to envision and appreciate the H-P system.

Adhering to the evolutionary H-P approach, we propose considering the prebasic moult, and perhaps the preformative moult, as ancestral to all modern bird lineages, having evolved from reptiles (Howell & Pyle 2015, Pyle 2022b; see also Kiat et al. 2020, 2021; Figs. 1, S1). The complete or near-complete prebasic moult occurs in all current-day avian taxa and, rather than simply a replacement of feathers, appears to be part of an endogenous restoration of body tissues (Voitkevich 1966, Murphy 1996, Kuenzel 2003) that may be ancestral to all vertebrates (King 1972). Considering the prebasic moult as homologous among modern birds is thus a parsimonious hypothesis, providing a robust nomenclatural framework that can be applied to

all bird moults and plumages. The preformative moult also appears to be present in most if not all modern bird lineages, and may have evolved in reptiles as body size developed quickly in the first year of life; if not, it evolved early in avian evolution as it is found in most or all basal lineages (Figs. 1, S1). Assuming homology among all modern bird taxa, the prebasic and preformative moults can provide the framework for defining all subsequently evolved moults within the H-P system (Figs. 1, S1). Additional inserted moults, including prealternate and presupplemental moults, can evolve (both appearing and disappearing) along bird lineages such that, unlike prebasic and preformative moults, they should not be considered homologous across all birds (Howell et al. 2003, Johnson and Wolfe 2018, Pyle 2022b).

Once an evolutionary basis is appreciated, moult strategies become substantially easier to compare across all species and latitudes. For example, the four underlying strategies identified by Howell et al. (2003), which are defined by the number of moults that occur within the first and later moult cycles, can be provisionally placed in an evolutionary context (Fig. 1; see Supporting information file and Fig. S1 for details). Although it is quite possible that inserted moults may have disappeared without trace along some bird lineages, envisioning how these four strategies may have evolved for current taxa has the potential to help inform a greater appreciation for the adaptive causes of inserted moults (Figure S1).

We contend that the evolutionary (H-P) system is more applicable on a global basis for studying avian moult than is the life-cycle system, and we thus encourage those who use the life-cycle system to also attempt visualizing an evolutionary approach to moult terminology, rather than trying to simply synonymize H-P terms with life-cycle terms. We suggest first determining the prebasic moult cycle, then whether or not inserted moults occur in the first and/or later cycles, and using an evolutionary approach to infer the correct designation of each inserted moult. Once envisioned, learned, and appreciated, the evolutionary approach proposed by Humphrey & Parkes (1959), as modified by Howell et al. (2003), is scientifically more precise, allows the recognition of all inserted moults, and is easier to apply consistently, to all taxa and by all parties interested in the study of moult in birds. We provide more detail on taking an evolutionary approach in the Supporting information file.

Figure Legend

Figure 1. A theoretical evolutionary approach to moult in birds from reptiles, using the four moult strategies defined by Howell et al. (2003; see also Howell 2010). The phylogenetic tree is based primarily on that of del Hoyo & Collar (2014, 2016) with some revisions to reflect recent systematic advancements (see Supporting information file for the use of this tree during times of phylogenetic flux). The four strategies are Simple Basic (SBS; no preformative or prealternate moults), Complex Basic (CBS; a preformative moult but no prealternate moults), Simple Alternate (SAS; a single moult in the first cycle and prealternate moults in later cycles), and Complex Alternate (CAS; a preformative moult in the first cycle and prealternate moults in all cycles). Here we propose that both prebasic and preformative moults, and hence the Complex Basic Strategy (purple lineages in the figure), are ancestral to all modern birds, although further study is needed on when preformative moults evolved in primitive avian taxa or reptiles ancestral to birds. Prealternate (and presupplemental) moults have evolved many times along different lineages and should not be considered homologous. See Supporting information file for an expanded version of this phylogenetic tree (Fig. S1) along with detailed explanation and discussion.

Data Availability Statement

There are no data associated with this manuscript.

ETHICAL NOTE

None.

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