

COMMENTARY

INCORRECT USE OF THE HUMPHREY-PARKES MOLT AND PLUMAGE TERMINOLOGY FOR BUNTINGS OF THE GENUS *PASSERINA*¹

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Recently, three excellent studies have identified hitherto unknown molts and plumages of the Indigo Bunting, *Passerina cyanea* (Rohwer 1986), the Painted Bunting, *P. ciris* (Thompson 1991), and the Lazuli Bunting, *P. amoena* (Young 1991). These authors explored hypotheses regarding the possible adaptive functions of the resulting plumages. All claimed to follow the system of nomenclature for molts and plumages proposed by Humphrey and Parkes (1959), but in fact did not do so. Since the Humphrey-Parkes (H-P) system was intended to be adaptable to all patterns of plumage succession and to reflect homologies between diverse groups of birds (Humphrey and Parkes 1959:14, 1963:499-500), correct adherence to the principles of that system is important. Therefore, I propose the correct application of the H-P system and discuss questions concerning plumage nomenclature in these buntings.

These authors described a molt involving some or all of the body feathers that occurs very soon after the birds fledge, which they correctly termed the First Prebasic molt. The H-P system requires that the replacement of the Juvenal plumage be termed the First Prebasic molt, and the resulting first non-juvenal plumage be the First Basic plumage (Humphrey and Parkes 1959, Palmer 1972). Clearly, when this period of molting stops, the First Prebasic molt is not finished, but has yet to replace those remaining juvenal body feathers as well as the juvenal remiges and rectrices. This is because the H-P system defines *plumage* as a single generation of feathers, as determined by how many times the feather follicles have actively produced feathers, not by when the feathers are worn during the bird's life (Humphrey and Parkes 1959:3-4). As a consequence, *molt* is defined as the shedding of one generation of feathers, and replacement of this generation by a new one (Humphrey and Parkes 1959:6). Thus, when a period of molting involves replacement of two or more generations of feathers, two or more distinct molts occur and must be accounted for (Humphrey and Parkes 1959:6-7).

The next period of molting in these buntings is of principal interest to these authors, for they hypothesize

that the resulting and subsequent feather coverings perform special adaptive functions. This molting renews all body feathers (except some primary coverts), all rectrices, the outer 4-7 primaries, and inner 3-6 secondaries. They call this period of molting the "Presupplemental" molt, which produces a "Supplemental" plumage, and they explicitly refer to the replacement of the remaining juvenal body feathers and the juvenal remiges and rectrices as part of this "Presupplemental" molt (Rohwer 1986:283, Thompson 1991:218-219, Young 1991:239-340). This is incorrect, because as stated above, the H-P system requires that these juvenal feathers be replaced in a First Prebasic molt. Therefore, what they have called a "Presupplemental" molt is actually a continuation of the First Prebasic molt, overlapping with a second molt that involves only those non-juvenal body feathers produced during the first part of the First Prebasic molt. The resulting feather coat of the bird is, therefore, a combination of two plumages: the First Basic and a later one, which might be called the "Supplemental." This is so because the H-P system leads to the interpretation that the First Prebasic molt of the juvenal remiges and rectrices is delayed, or offset, in timing, and this offset carries over into subsequent molt cycles (Palmer 1972:70, 87-88).

Calling the second molt "Presupplemental," which produces a "Supplemental" plumage, presents another problem. The definition of *supplemental plumage* is a third or subsequent plumage in a molt cycle (Humphrey and Parkes 1959:23-24, Palmer 1972:72-73). *Cycle* is defined as a sequence of molts and plumages that runs from one molt to the recurrence of that same molt, typically coinciding with an annual seasonal or reproductive cycle (Humphrey and Parkes 1959:2-3, Palmer 1972:67). Humphrey and Parkes applied this definition explicitly to adult birds (1959:3), so without a recurrence of a third molt and plumage in the cycles of older birds, calling one of the two molts in a young bird's first autumn "Presupplemental" is a novel use of the term, and should be justified. Using the term as have Rohwer, Thompson, and Young implies that the corresponding molt and plumage in older birds has been suppressed. Only Young (1991:239-240) offered justifications for using the term. He stated that the second molt of young birds represents a new molt that has been added to a previous sequence involving only one molt in the autumn, and that this molt in the Lazuli Bunting appears to be homologous to the corresponding molt in the Indigo Bunting, which Rohwer (1986) had already called the "Presupplemental." Such an extension of the definition of *supplemental plumage* to include any plumage that apparently has been added to a sequence of plumages but is not repeated in subsequent cycles, is a change that has significant effects on the determination of plumage homologies in the way Humphrey and Parkes intended (1959, 1963). This poses serious questions about the evolutionary processes that produced such a one-time "supplemental"

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plumage. That the "Presupplemental" molt "... is in addition to the presumably ancestral fall prebasic and spring prealternate molts..." (Young 1991:239) is but one of at least four alternative hypotheses about the evolution and homology of plumages in these buntings! To accept this hypothesis, we must reject the other three, namely: (1.) The second molt of body plumage is not an added plumage, but represents the ancestral First Prebasic molt, whereas the initial molt of body plumage in young birds is the added one that should be called the "Presupplemental." (2.) A "Presupplemental" molt does not exist. Rather, the second molt of body plumage is the First Prealternate molt, so that the spring molt of body plumage is the first part of the Second Prebasic molt, homologous with the first molt of juvenal body plumage. (3.) The newly added molt is the body molt occurring during the birds' first spring, and should be called the "Presupplemental" instead of the First Prealternate in order to reflect correct evolutionary relationships.

The first alternative seems to be as much a possibility as the one given by Young, except that the rules of the H-P system preclude it by defining the first nonjuvenal plumage as the First Basic, thus implying that this plumage is homologous with every other first basic plumage in the world. Extraordinary evidence showing this to be the "Presupplemental" molt would be required to accept this hypothesis while adhering to the H-P system. This is so even though the second molt seems to be physiologically equivalent to the complete prebasic molts of subsequent plumage cycles, and thus seemingly to be homologous with them.

The second alternative is the simplest, and requires no change of the H-P system. Indeed, when I discovered an analogous sequence of molts and plumages in Cassin's Sparrow, *Aimophila cassinii*, and Bachman's Sparrow, *A. aestivalis* (not two complete molts as stated by Young 1991:236) (Willoughby 1986), I used this hypothesis to classify the molts and plumages, following advice from Kenneth Parkes (letter) and Ralph Palmer (referee's comments on the manuscript). I discussed various hypotheses as to how such a pattern had evolved (Willoughby 1986:470). I was unsatisfied with this system because what in adult birds became the prebasic molt producing the basic body plumage, and the prealternate molt producing the alternate plumage, appeared to be physiologically and functionally equivalent to, and therefore probably homologous to, the prealternate and prebasic molts, respectively, of the majority of Emberizidae (Willoughby 1986:470). Acceptance of this homology makes the hypothesis of a new, never repeated "Presupplemental" molt attractive. Perhaps Rohwer accepted this hypothesis so as to preserve the apparent homology of the prebreeding and postbreeding molts of the Indigo Bunting to the corresponding seasonal molts of so many other passerine species. However, Humphrey and Parkes (1959, 1963) and Palmer (1972) explicitly cautioned against tying molt and plumage terminology and homology to seasonal and reproductive cycles instead of to the strict accounting of feather generations.

The third hypothesis, that a new, unrepeatable molt has been added after the second molt is as plausible as the one Young proposed for the Lazuli Bunting. There

is no *a priori* way to determine whether the added "Presupplemental" molt has been inserted after the First Basic plumage or after the First Alternate plumage. Humphrey and Parkes (1959:25) and Palmer (1972: 66, 72-73) clearly stated that a supplemental plumage can come before or after the alternate plumage. Arguments have to be advanced to show why this hypothesis should be rejected.

Rohwer, Thompson, and Young are not alone in mistaken use of the H-P system. For example, Pyle et al. (1987:12) mistakenly equated the basic plumage with "winter plumage" and alternate plumage with "summer or breeding plumage," and mistakenly stated that "Those [species] that lack a prealternate molt acquire their alternate plumage by the natural wearing of the tips of the contour (body) feathers." These ornithologists appear to use the H-P terminology superficially as a simple replacement for the terminology that was pioneered by Dwight (1900) and that is still widely favored internationally (see, for example, Cramp and Simmons 1977:30-31, Kasperek 1985). However, Humphrey and Parkes (1959, 1963) considered such a "dependent" terminology to be misleading and offered their system as a way around what they considered to be a serious defect.

Stresemann (1963) and Amadon (1966) argued against replacing the traditional, dependent, system of Dwight with the H-P system, pointing out, among other things, that the former incorporates much information about the life history events for which the molts and plumages are probably adapted by natural selection, and so organizes much useful information that is intentionally left out of the H-P system. I have argued (Willoughby 1991) that the H-P system should be abandoned in favor of the traditional terminology because, i) it is difficult to adapt to unusual molt sequences (as illustrated by these buntings), ii) the definition of *plumage* as a *single generation of feathers* is inappropriate for some emberizines of the genus *Spizella*, iii) using it as intended to determine homologies of plumages in various species leads to arbitrary suppression of reasonable hypotheses (such as alternative 1 above), and iv) because it contains no information on the life cycle events to which the plumages are probably adapted. Homologies can still be determined on the basis of the physiological, biochemical and anatomical characteristics of the molts and feathers, that is, those characteristics that are more likely to reflect inheritance from common ancestry than the simple numerical order of occurrence of molts and plumages in the life of the bird.

Because Rohwer, Thompson, and Young are primarily interested in the adaptive functions of the various plumages of buntings, I recommend that they apply terms to the molts and plumages that connect them with the critical life-history events. Thus, calling the plumage that is worn by the buntings in their first spring and summer the "First, or Immature, Breeding plumage" acquired by a "First Prebreeding molt" conveys much more information about its relationship to ecological and selective factors than calling it the "First Alternate," "Second Basic," or "Supplemental," whichever the case might be. At the very least, investigators who decide to use the H-P terminology should

do so according to the rules clearly specified by its authors.

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CLARIFYING THE HUMPHREY-PARKES MOLT AND PLUMAGE TERMINOLOGY¹

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In recent studies of the sequences of molts and plumages of Indigo Buntings, *Passerina cyanea* (Rohwer 1986), Painted Buntings, *Passerina ciris* (Thompson 1991), and Lazuli Buntings, *Passerina amoena* (Young 1991), we employed the nomenclature for molts and plumages recommended by Humphrey and Parkes (1959). Willoughby (1992) criticizes several aspects of our use of the Humphrey and Parkes (H-P) system and also challenges the way in which we have implicitly homologized the plumages of these buntings with those of other birds. All of Willoughby's criticisms stem from confusion over how to apply the H-P terminology correctly when describing a species' molts and plumages. Here we provide a brief overview of the process one goes through when naming molts and plumages under the H-P system. We hope this will clarify confusion regarding use of the system. Applying the H-P terminology correctly is critical when identifying molt homologies across diverse taxa and when using plumage data to infer age in ecological studies. Throughout, we will use examples from the three species of buntings that we studied.

The sequence of molts and plumages in Indigo, Painted, and Lazuli Buntings is the same, although the timing and extent of their molts differ (see Young 1991: Table 5). After fledging, young buntings replace some to all of their juvenal body plumage in a first prebasic molt. Shortly thereafter, they undergo another episode of molt in which they replace all of their first basic body plumage, all retained juvenal body feathers (if any), all juvenal rectrices, and some of the juvenal primaries and secondaries. We call this the presupplemental molt and the resulting plumage the supplemental plumage. In winter and spring these birds molt a third time, replacing some to all of the supplemental body plumage in their first prealternate molt. After this,

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