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

LITERATURE CITED

AMADON, D. 1966. Avian plumages and molts. Condor 68:263–278.

CRAMP, S., AND K. E. L. SIMMONS. 1977. Handbook of the birds of Europe, the middle East and North Africa. The birds of the western palaearctic. Vol. 1. Oxford Univ. Press, Oxford, England.

DWIGHT, J., JR. 1900. The sequence of plumages and moults of the passerine birds of New York. Annals N.Y. Acad. Sciences 13:73–360. (reprinted 1975)

HUMPHREY, P. S., AND K. C. PARKES. 1959. An approach to the study of molts and plumages. Auk 76:1–31

HUMPHREY, P. S., AND K. C. PARKES. 1963. Comments on the study of plumage succession. Auk 80:496–503.

KASPAREK, M. 1985. Über die Mauser der Vögel, p. 69–91. *In* H. Bub [ed.], Kennzeichen und Mauser europäischer Singvögel. Die Neue Brehm-Bücherei, A. Ziemsen Verglag, Wittenberg Lutherstadt.

PALMER, R. S. 1972. Patterns of molting, p. 65–102. *In* D. S. Farner and J. R. King [eds.], Avian biology. Vol. 2. Academic Press, New York.

PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.

ROHWER, S. 1986. A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. Auk 103:281–292.

STRESEMANN, E. 1963. The nomenclature of plumages and molts. Auk 80:1–8.

THOMPSON, C. W. 1991. The sequence of molts and plumages in Painted Buntings and implications for theories of delayed plumage maturation. Condor 93:209–235.

WILLOUGHBY, E. J. 1986. An unusual sequence of molts and plumages in Cassin's and Bachman's sparrows. Condor 88:461–472.

WILLOUGHBY, E. J. 1991. Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. Proc. West. Found. Vertebr. Zool. 4:247–286.

YOUNG, B. E. 1991. Annual molts and interruption of the fall migration for molting in Lazuli Buntings. Condor 93:236–250.

The Condor 94:297–300

CLARIFYING THE HUMPHREY-PARKES MOLT AND PLUMAGE TERMINOLOGY[1]

SIEVERT ROHWER, *Burke Museum DB-10 and Department of Zoology, University of Washington, Seattle, WA 98195*
CHRISTOPHER W. THOMPSON,[2] *Department of Zoology, Arizona State University, Tempe, AZ 85287-1501*
BRUCE E. YOUNG, *Burke Museum and Department of Zoology NJ-15, University of Washington, Seattle, WA 98195*

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,

[1] Received 21 October 1991. Accepted 22 October 1991.

[2] Present address: Burke Museum DB-10 and Department of Zoology, University of Washington, Seattle, WA 98195.

they undergo two molts per year, a definitive prebasic molt following breeding, which is complete, and a definitive prealternate molt prior to breeding, which is incomplete.

NAMING MOLTS AND PLUMAGES

How does one go about naming the molts and plumages of a bird? The key is in determining homologies, both with other species and between age classes within species. First, one identifies the molts and resulting plumages that occur during a bird's life, keeping in mind the H-P definitions of molt and plumage. A *molt* is "the normal *shedding of feathers and the replacement of most or all of these by a new generation of feathers*" (Humphrey and Parkes 1959:6). A single molt produces a single generation of feathers regardless of which feathers are replaced. A *plumage* is "a single generation of feathers" (Humphrey and Parkes 1959:4) that grows in during a single molt. A *generation* of feathers is thus the same as a plumage. If a molt is not complete, then the newly grown feathers represent one generation (plumage) that is distinct from the generation (or generations) of feathers that were not replaced in that molt.

The next step is to determine the plumage cycle for the species in question. A cycle is the time period that "runs from a given plumage or molt to the next occurrence of the same plumage or molt" (Humphrey and Parkes 1959:3). This is usually a year in temperate birds, but may be more or less in certain tropical or oceanic species (Humphrey and Parkes 1959). Since Humphrey and Parkes wrote we have learned that various features of the first and later plumage cycles may differ (e.g., number of molts); nonetheless, we assume that the molts held in common between first and later plumage cycles can be homologized.

Armed with this information, one is ready to assign names to the molts and plumages of the first and later cycles. Critical to this process is the number of molts per cycle, which is equal to the number of times the most active set of feather follicles undergoes renewal per cycle. If there is only one molt per cycle, it is called a prebasic molt that gives rise to basic plumage. If there are two molts per cycle, one is a prebasic molt and the other a prealternate molt. These respectively give rise to the basic and alternate plumages. How does one decide which is which? This is accomplished using molt homologies. One compares the timing, extent, and color change in each molt with that of closely related species that have already been described. If there is one complete and one incomplete molt, then the complete molt usually will be the prebasic molt and the incomplete molt usually will be the prealternate molt. This, however, is only a guide; we believe that investigators should always base their final decision on homologies rather than rules. If there are two complete molts, one uses timing and color information to homologize with other species. If there are three molts per cycle, there is a presupplemental molt in addition to the prebasic and prealternate molts. Molts are still named based on homologies. If a species has three molts per cycle but its close relatives have only two molts per cycle, then the presupplemental molt is the one molt that is not homologous to either of the two molts known in its relatives. Other special cases are dealt with in Humphrey and Parkes (1959) that need not be discussed here.

Willoughby's criticisms are based on his mistaken definitions of molt and plumage (and therefore generation). Willoughby (1992:295–297) defines molt as "the shedding of one generation of feathers, and replacement of this generation by a new one." This definition leads him to conclude that "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" (Willoughby 1992:295–297). Thus, he believes that we violated H-P nomenclature for molts by giving only one name (presupplemental molt) to the molt episode in which body feathers are replaced for the *second* time and remiges and rectrices are replaced for the *first* time. Yet, as Humphrey and Parkes state, "the feathers which are shed during a given molt may belong to a single generation or may include feathers, belonging to earlier generations, which have survived one or more previous molts" (Humphrey and Parkes 1959:6). Thus, we correctly defined the feathers replaced in the presupplemental molt as a single plumage since they are all produced in the same molt, even though this molt involves the loss of more than one generation of feathers. Willoughby's definition of plumage, "a single generation of feathers, as determined by how many times the feather follicles have actively produced feathers" (Willoughby 1992: 295–297) is therefore incorrect. The key difference between this and Humphrey and Parkes' definition is that Willoughby relies on when the feathers are lost rather than on when the feathers are grown to define a plumage.

Similarly, Willoughby is also misleading when he states that the H-P system requires that the only molt that can replace juvenal plumage is the first prebasic molt. Thus, Willoughby asserts that the first prebasic molt begins during a bird's first fall and continues in a series of temporally disjunct molts, which span more than a year, until all juvenal feathers are replaced. Besides being confusing and contradictory to the definition of molt, this is certainly counter to Humphrey and Parkes who specifically state "several molts may be involved in the replacement of all of the juvenal feathers. . . . We conceive of the total postjuvenal feather replacement as being accomplished in one or more 'pre-'molts" (Humphrey and Parkes 1959:15).

CHARACTERIZING AGE WITHOUT VIOLATING DEFINITIONS

Humphrey and Parkes restrict the definition of plumage to a single generation of feathers within a plumage cycle. This concept may be confusing to those who are unfamiliar with H-P nomenclature because most people erroneously think plumage is synonymous with a bird's entire covering of feathers or "feather coat" (Humphrey and Parkes 1959:5–6). By the restricted definition employed by Humphrey and Parkes, a male Lazuli Bunting in its first potential breeding season is in first alternate "plumage." This plumage, however, includes only some feathers of the head. Having "survived" both the first prebasic and presupplemental molts, its inner primaries and outer secondaries are part of the retained juvenal plumage. The outer pri-

maries, inner secondaries, rectrices, and most of the body feathers are part of the supplemental plumage, because these feathers were replaced in the presupplemental molt but not in the first prealternate molt.

Thus, from the statement that a bird is "in X plumage," all that can be inferred is that it has completed the molt that produces that plumage. The entire feather coat is made up exclusively of that plumage only if the antecedent molt in that plumage cycle was complete.

APPLYING THE TERM *SUPPLEMENTAL* TO THE FIRST PLUMAGE CYCLE

Willoughby criticizes our use of the term supplemental for one of the three molts and plumages of the first plumage cycle of buntings. He does so because Humphrey and Parkes referred to supplemental plumages only with regard to adult birds. However, Humphrey and Parkes do not restrict the use of the term supplemental to adult birds. Rather, they (1959:15–16) state that "a few species have evolved a cycle in which, as 'adults,' more than two molts occur. . . . Such a plumage may be inserted in the typical two-plumage cycle either before or after the alternate plumage; its position will depend on the functional basis for the evolution of such an additional plumage." Humphrey and Parkes (1959) probably discuss supplemental plumages only with regard to adult birds simply because molts additional to the prebasic and prealternate were known only for adults at the time they wrote. We see no reason to apply a special term to such an additional molt merely because it occurs in first but not later plumage cycles. As Humphrey and Parkes wrote (1959:17): "We are well aware that difficulties will be encountered in applying this terminology to certain groups of birds. In some cases this will prove to be due to incomplete knowledge of the molts and plumages of that group. . . . Other cases may well show that parts of our fundamental thesis need to be altered or broadened."

Interestingly, Willoughby (1986) has also documented the existence of three distinct plumages in the first plumage cycle of Cassin's, *Aimophila cassinii,* and Bachman's Sparrows, *A. aestivalis.* As in our buntings, this additional plumage does not exist in adults. By avoiding calling this additional immature plumage "supplemental," Willoughby had to apply the awkward term "second prebasic" to the last of the three molts of *the first plumage cycle* (see Willoughby 1986:Fig. 4). The consequence is that between-species homologies are lost in the definitive plumage cycle. By refusing to name one of the first-year plumages *supplemental,* the next name that Willoughby finds available under the Humphrey and Parkes system for naming the first fall molt of adults sparrows is *second pre-alternate.* This is precisely the molt that is presumably homologous with the second (often definitive) prebasic molt of other birds. In both Cassin's and Bachman's Sparrows, this molt not only occurs after breeding, but is also complete. Both points are evidence of its homology with the fall molts of other passerines, which Willoughby (1986:470) himself acknowledges. We see this not as a failure of the Humphrey and Parkes system but as a failure to use it exactly as it was originally intended, namely to track molt and plumage homologies. Freeing the terminology from seasonal and reproductive cycles was rightly observed by Humphrey and Parkes to be necessary for homologizing the molt and plumage cycles of waterfowl with those of other birds. But this does not mean that such information should be ignored entirely in establishing homologies and naming plumages when cycles more complex than those imagined by Humphrey and Parkes are discovered. Willoughby's 1986 discovery is exciting but difficult to appreciate because of his choice of terminology. Ironically, Willoughby's incorrect interpretations of the Humphrey and Parkes system lead him to advocate Dwight's (1900) system of naming molts and plumages that leaves out all information about among-species molt and plumage homologies (Willoughby 1992).

UNTREATED ALTERNATIVES

Willoughby's final criticism is of our explicit (Young 1991) or implied (Rohwer 1986, Thompson 1991) conclusion that the molt we identified as the presupplemental is truly the "new" molt and, thus, that the other two molts in the first plumage cycle are the ancestral prebasic and prealternate molts. We neither discussed this satisfactorily nor excluded possible alternative hypotheses, so Willoughby's criticism is justified. We take this opportunity to explain our logic.

First, we must consider whether there really is a novel molt in the first plumage cycle of buntings. If we assume, as does Willoughby, that there is no presupplemental molt in the first plumage cycle, then this cycle can include only the first two molts. The first molt would remain the prebasic molt since its timing, extent, and lack of dramatic color change make it homologous to the first fall molt of related passerines. The second molt would then have be called the first prealternate because this is the only remaining name. This would be incorrect for two reasons. First, the molt occurs at the beginning of the winter, not the end as do the prealternate molts of most other temperate passerines. Second, very few passerines molt remiges or rectrices in the first prealternate molt but not in later prealternate molts. An even more fundamental problem with assuming the first cycle includes only the first two molts is that the adult cycle must then begin with the third molt undergone by first-year birds. Since this third molt is incomplete and occurs in spring, by molt homologies, it should be named the second prealternate molt. Since cycles should begin with the same molt (and the first cycle begins with a prebasic molt), this implies that a second prebasic molt that once occurred *before* the so called second prealternate molt has been lost. Such a scenario is so untenable that the only sensible conclusion is that the first plumage cycle involves three molts, one being novel.

Next, as Willoughby observes, the fundamental issue is which molt is novel relative to the ancestral first molt cycle which we have implicitly assumed featured just two molts. First consider the novel molt as if it had been inserted prior to the first prebasic molt. In Indigo and Painted Buntings this seems unlikely because nothing about their first molt of pennaceous feathers is strikingly different from that of other passerines. It is a complete molt of body plumage but excludes remiges and rectrices. Thus, considering it the first prebasic molt was consistent with the H-P definition and did not violate apparent homologies since

many other passerines do not replace remiges or rectrices in their first prebasic molt. We emphasize, however, that molt homology was the reason we named this molt the first prebasic molt, not the fact that it is the first molt to replace juvenal feathers.

Similarly, we rejected the possibility of naming the first spring molt of body feathers *presupplemental* based on the following homologies. First, the timing, extent, and change in plumage color is essentially identical to that of the definitive prealternate molt in adult buntings. Second, naming the third (spring) molt presupplemental would require naming the second molt as the first prealternate molt. But the second molt differs radically from the definitive prealternate molt in timing, in extent, and in the color change it produces, both in the buntings we studied, and in most other passerines. Thus, naming the third molt presupplemental would imply the origin of many new character states in the second molt that could not be homologized with the prealternate molt of other passerines.

The molt that each of us discovered as being unique to the first plumage cycle of a different species of *Passerina* is unusual in three ways, all of which justified calling it the presupplemental molt. First, it is the second molt of body plumage that takes place in the first fall. Second, it includes the replacement of outer but not inner primaries. Third, it results in first-year male Indigo Buntings assuming in mid-winter a plumage that matches the moderately conspicuous plumage of adult males, rather than the brown plumage worn by all females and by males in first basic plumage. All of these special features of this second molt suggest that it, rather than the first or third of the three molts of the first plumage cycle, is the evolutionary novelty. We thus reject all of Willoughby's alternative hypotheses even though we fully admit that we failed to treat them explicitly in our original papers.

Had Lazuli Buntings been the only one of these three species to be studied, identifying the novel molt would have been more difficult. This is so because their first prebasic molt of body plumage is incomplete. Incomplete replacement of the juvenal body plumage is unusual in passerines, but we speculate here that it may have been "permitted" because of the prior evolution of the presupplemental molt. The selective force favoring the reduction in extent of the first prebasic molt of Lazuli Buntings (Young 1991) may be the very dry conditions of their breeding grounds in late summer (see Rohwer and Manning 1990).

Willoughby's (1986) discovery of a presupplemental molt in the first plumage cycle of two emberizine sparrows raises larger questions about the origin of this molt than any of us have considered. Rohwer (1986) implicitly assumed that the presupplemental molt was unique to certain cardinaline buntings and argued that it existed in Indigo Buntings to enable young males to become mimics of adult males in early winter. While this molt does produce such a color change, Willoughby's (1986) discovery of a probable homologous molt in two emberizine sparrows, neither of which significantly changes color in molting from first basic to supplemental plumage, challenges Rohwer's assumption that this molt originated to effect color changes. In combination, our studies of *Passerina* and Willoughby's investigation of *Aimophila* suggest that this molt may be a shared derived character of widespread occurrence, both within the Emberizidae and possibly in other families of passerines. Thus, before reasonable hypotheses of origin can be developed, we need to know more about its phylogenetic distribution. Among the Emberizidae, the next most important species to investigate would be those in lineages that diverged earlier than the split between *Aimophila* and *Passerina*. Following Sibley and Ahlquist (1990), we would suggest the Olive Warbler, *Peucedramus taeniatus*, and the Yellow-breasted Chat, *Icteria virens*.

We thank K. C. Parkes and P. S. Humphrey for helpful discussions and correspondence.

LITERATURE CITED

DWIGHT, J., JR. 1900. The sequence of plumages and moults of the passerine birds of New York. Annals N.Y. Acad. Sciences 13:73–360. (reprinted 1975).

HUMPHREY, P. S., AND K. C. PARKES. 1959. An approach to the study of molts and plumages. Auk 76:1–31.

ROHWER, S. 1986. A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. Auk 103:281–292.

ROHWER, S., AND J. MANNING. 1990. Differences in timing and number of molts for Baltimore and Bullock's Orioles: implications to hybrid fitness and theories of delayed plumage maturation. Condor 92:125–140.

SIBLEY, C. G., AND J. E. AHLQUIST. 1990. Phylogeny and classification of birds. Yale Univ. Press, New Haven, CT.

THOMPSON, C. W. 1991. The sequence of molts and plumages in Painted Buntings and implications for theories of delayed plumage maturation. Condor 93:209–235.

WILLOUGHBY, E. J. 1986. An unusual sequence of molts and plumages in Cassin's and Bachman's sparrows. Condor 88:461–472.

WILLOUGHBY, E. J. 1992. Incorrect use of the Humphrey-Parkes molt and plumage terminology for buntings of the genus *Passerina*. Condor 94:295–297.

YOUNG, B. E. 1991. Annual molts and interruption of the fall migration for molting in Lazuli Buntings. Condor 93:236–250.