

DETERMINING HOMOLOGY OF MOLTS AND PLUMAGES TO ADDRESS EVOLUTIONARY QUESTIONS: A REJOINDER REGARDING EMBERIZID FINCHES¹

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Abstract. Determining how molt is integrated into the annual cycle, and understanding what natural selection pressures have favored the diversity of molt strategies in birds are important issues in ornithology and zoology in general. To study these issues, most ornithologists historically have used and continue to use many different nomenclatural systems which tie names of molts and plumages (e.g., breeding plumage, summer plumage, adult plumage) to events in the annual cycle, season or age. However, it is circular to study the evolution of molts and plumages in relation to annual cycle events, seasons or age because the definitions of plumages and molts in these systems are defined in terms of these parameters. To study the evolution of molts and plumages it is essential to use a system such as that proposed by Humphrey and Parkes (1959, 1963) to identify homologous molts and plumages that is independent of annual cycle events, seasons and age. This paper discusses how to use correctly the Humphrey-Parkes system and illustrates this by discussing an example of how the Humphrey-Parkes system was applied incorrectly in a series of studies on *Passerina* buntings. We also document that *Phainopepla*, *Phainopepla nitens*, Yellow-breasted Chats, *Icteria virens*, Northern Cardinals, *Cardinalis cardinalis*, and Orange-breasted Buntings, *Passerina leclancherii* exhibit a previously unknown sequence of molts and plumages that is homologous to that of other recently studied *Passerina* species, and suggest that this sequence of molts and plumages probably is much more widespread in birds than is currently recognized.

Key words: Molt; plumage; nomenclature; homology; *Passerina*; evolution; life history.

INTRODUCTION

Natural selection has favored many species of birds to wear plumages with different color patterns (1) in the breeding versus nonbreeding seasons, (2) at different ages, and (3) in males versus females (Rohwer and Butcher 1988, Butcher and Rohwer 1989). To accomplish such changes in plumage color, birds must replace their feathers by molting (Palmer 1972, Payne 1972). In addition, feathers of all birds become worn with age, and must be replaced to function properly during flight and for thermoregulation. Thus, molt plays an important role in the ecology (i.e., annual cycle) of birds and, therefore, in the evolution of their life histories. Similarly, in addition to the obvious physiological costs of molt (recrudescence of the integument, keratin synthesis, reduced thermoregulatory ability and decreased flight efficiency), the molting process also entails significant changes in many other less obvious physiological processes including bone and pro-

tein metabolism, hematopoiesis, and water balance and the hormonal regulation of these processes (e.g., Rehder et al. 1982). To meet the physiological demands of molt, birds may increase their basal metabolic rate as much as 60–80% and their daily energy expenditure nearly 50% above their respective levels when they are not molting or breeding (Payne 1972, Murphy and King 1992). Whether increases in basal metabolic rate and daily energy expenditure associated with molting constitute an energetic “stress” (i.e., cause nutrient demands to exceed nutrient ingestion, resulting in a net catabolism in body tissues to the extent that one or more vital physiological functions are impaired [King and Murphy 1985]) varies widely among ecologically and phylogenetically diverse avian taxa and is much debated (King 1980, Walsberg 1983a, King and Murphy 1985, Murphy and King 1991a, Earnst 1992, Hohman et al. 1992, Gates et al. 1993, Moorman et al. 1993). However, molt clearly is energetically stressful in at least some species (Brown 1985, Groscolas and Cherel 1992, Thompson and Walsberg 1993). All aspects of the molting process must be subject to strong

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selection pressures for three reasons: (1) plumage color often facilitates social signaling or crypsis (Rohwer and Butcher 1988, Butcher and Rohwer 1989), (2) structurally sound flight feathers and body plumage are necessary for efficient flight performance (e.g., Rutledge 1979, Dorka 1981, Burt 1986, Noordhuis 1989, Spearman and Hardy 1985, Tucker 1991) and thermoregulation, respectively (e.g., Spearman 1980; Walsberg 1981, 1982, 1983b, 1988a, 1988b; Spearman and Hardy 1985; Cena et al. 1986; Furness and Burger 1988; Piersma 1988), and (3) molting imposes large physiological and energetic demands on birds (discussed above).

Thus, molt, along with reproduction and migration (in migratory species), constitutes one of the two or three most important features of the annual cycle in birds. An understanding of both the proximate and ultimate bases of the molting process, and quantitative documentation of the sequence of molts and plumages in birds, are essential for addressing many basic and applied issues in biology including the following. (1) Aging and sexing birds correctly which is an essential prerequisite for nearly all studies (e.g., Taber 1963, Madsen 1967, Prater et al. 1977, Busse 1984, Pyle et al. 1987, Carney 1992, Svensson 1992, Baker 1993, Mulvihill 1993). (2) Constructing life tables from estimates of differential survivorship among age and sex classes. This is necessary, for example, for calculating sustainable harvest limits for management of game species (Carney 1984, Crissey 1984). (3) Determining timing and route of migration, which is especially important for the conservation and management of species which use staging areas during migration for feeding or molting (Jehl 1990). (4) Evaluating the relative health of individuals in populations with ptilochronology (Grubb 1989, 1992, in press a, in press b; Murphy and King 1991b; Murphy 1992; Yosef and Grubb 1992, in press; Brodin 1993; Grubb and Pravosudov 1994). (5) Documenting the effect of diet (e.g., carotenoid pigments) on plumage color (Goodwin 1984; Partali et al. 1987; Brush 1990; Hill 1992, 1993; Hudon 1994; Thompson et al., unpubl. manuscript). (6) Determining the effect of abiotic factors (e.g., daylength [e.g., Chilgren 1978], temperature [e.g., Rouanet and Barre 1982, Rymkevich and Ryzhanovsky 1987, Ewins 1988, Groscolas and Chérel 1992]), food availability (Gaston 1981), social environment (e.g., status in dominance hierarchy [e.g., Myhre

1980]), ecto- and endoparasites (e.g., Loye and Zuk 1991, Zuk 1992), pollution (e.g., Furness et al., 1986, Braune 1987), genetics (e.g., Berthold 1985), and internal environment (e.g., hormone levels [Witschi 1961, Smith 1982, Stokkan et al. 1986, John et al. 1988]) on timing, rate, and extent of molt.

Despite the obvious importance of (1) documenting the sequence of molts and plumages of birds for the reasons discussed above, (2) determining how molt is integrated into the annual cycle of birds, and (3) understanding what natural selection pressures have favored the diversity of molt strategies observed in birds, the sad reality is that the literature regarding molts and plumages of most species usually is scanty and incomplete, often contains major errors or contradictions among sources, and usually is confined to studies in only a small part of the species geographic range which does not necessarily reflect the biology of the species throughout its range (e.g., Pyle et al. 1987 and references cited therein).

Most of our lack of knowledge can be traced to two causes. (1) Most museum collections contain mostly non-molting adult (i.e., definitive-plumaged [Humphrey and Parkes 1959]) birds, especially males, collected on the breeding grounds (e.g., North America), but have very few birds in molt or in predefinitive plumages. (2) Molt has been and remains an unpopular research topic. For example, of all ornithological literature indexed in *Wildlife Review* (87,417 citations; approximately 1970 through February 1994), a database produced by the U.S. Department of Interior that indexes both governmental and non-governmental fish and wildlife literature, only 1.2% discuss molt to any degree whereas 4.2 times (4.9%) and 10.5 times (12.3%) as many citations address migration and reproductive biology, respectively, as their primary focus. Similarly, of all ornithological literature indexed in *Zoological Record* (143,266 citations; 1978 through 1993), an international database of zoological literature, only 1.2% discuss molt to any degree whereas 6.6 times (7.8%) and 17.3 times (20.4%) as many citations address migration and reproductive biology, respectively, as their primary focus.

One obstacle to advancing our knowledge of the sequence of molts and plumages of birds and the evolution of these molt and plumage patterns is that ornithologists historically have used and

continue to use many different systems to name molts and plumages. Some follow Dwight's (1900a, 1902, 1905) system which ties names of molts and plumages to events in the annual cycle, e.g., postjuvenile molt and prenuptial molt (e.g., Cramp et al. 1977 and subsequent volumes, Ginn and Melville 1983). Some use names associated with seasons, e.g., summer and winter plumage (Prater et al. 1977). Some use names tied to ages, e.g., juvenile, immature and adult plumage (Witherby et al. 1943 and subsequent volumes), and some use combinations, e.g., age and season (Svensson 1992). Although such systems may be adequate for some purposes, all of these systems are unsuitable for addressing most questions regarding evolution of molts and plumages for two reasons. First, these systems name molts and plumages *in terms of* annual cycle events, seasons or age rather than *in relation to* them, as suggested by Humphrey and Parkes (1959, 1963). Thus, it is not possible to investigate the relationship between molt and annual cycle events, seasons or age because the definitions of plumages and molts are not independent of these parameters but, rather, are defined in terms of them. As a result, evolutionary patterns that might emerge through comparative studies have been and continue to be obscured. Second, to study the evolution of molts and plumages it is essential to identify homologous molts and plumages among the taxa of interest. It is not possible to identify homologies among molts and plumages of related taxa with the systems discussed above that employ dependent nomenclature (see Humphrey and Parkes 1959, 1963 for more detailed discussion).

Humphrey and Parkes (1959, 1963) recognized that insights into the evolution of molts and plumage patterns can only be gained by identifying homologous molts and plumages among related taxa. In turn, they also recognized that determining homologies requires employing a nomenclatural system that is independent of annual cycle events, seasons and age. With remarkable foresight and clarity, Humphrey and Parkes (1959, 1963) proposed such a system (explained below).

The purpose of this paper is to discuss how to use correctly the Humphrey-Parkes (hereafter H-P) system to identify homologous molts and plumages to address evolutionary questions, and to illustrate this by discussing an example of how the Humphrey-Parkes system was applied in-

correctly in a series of studies on *Passerina* buntings.

Previous recent studies of Indigo, *Passerina cyanea*, Lazuli, *P. amoena*, and Painted Buntings, *P. ciris*, documented that they undergo a sequence of molts and plumages during their first few months of life that had never been demonstrated in any other bird species previously (Rohwer 1986; Young 1991; Thompson 1991a, 1991b, 1992). Between hatching and the beginning of their first potential breeding season, when they are about ten months old, young buntings undergo three molts (described below), not including their first (prejuvenile) molt which replaces natal down with juvenal plumage. Rohwer (1986), Thompson (1991a, 1991b) and Young (1991) followed the terminology of Humphrey and Parkes (1959) and named these molts first prebasic, presupplemental and first prealternate in that order (Fig. 1), for reasons described below. Subsequent studies of other species in which we have discovered similar molt and plumage sequences (Thompson and Leu, in press, unpubl. data), have convinced us that the second molt (named presupplemental previously) is homologous with definitive prebasic molt, and that the first molt (named first prebasic previously) is a presupplemental molt, i.e., not homologous to any molt in subsequent molt cycles. As a result, the names of the first two molts should be reversed, i.e., the second molt should be named the first prebasic molt and the first molt should be named the presupplemental molt (Fig. 1).

We summarize below the sequence of molts and plumages in *Passerina* buntings, review the logic of the H-P system for naming molts and plumages, explain how Rohwer (1986), Thompson (1991a), Young (1991) and Rohwer et al. (1992) used the H-P system to assign names to these molts and plumages, present new data that indicate why the names assigned to the first two molts are incorrect and should be reversed (Fig. 1), and discuss the superiority of the H-P system over other nomenclatural systems for studying the evolution of molt and plumage sequences in birds.

SEQUENCE OF MOLTS AND PLUMAGES IN *PASSERINA*

Within a few days after fledging, young *Passerina* buntings begin a rapid molt lasting three to four weeks during which they replace most to all of their juvenal body plumage with another plum-

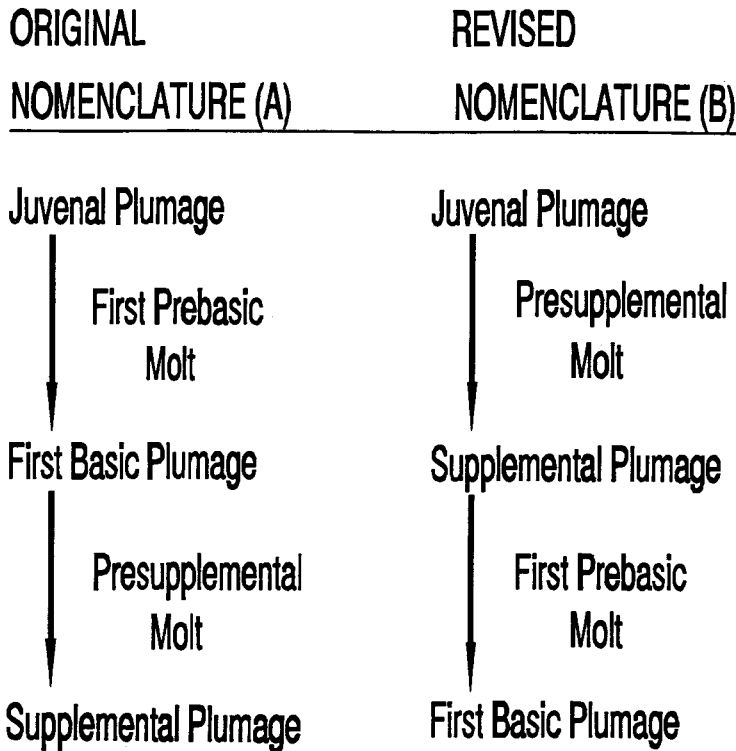


FIGURE 1. Diagram of the (A) names originally assigned to the sequence of molts and plumages of Indigo, *Passerina cyanea*, Lazuli, *P. amoena*, and Painted Buntings, *P. ciris*, by Rohwer (1986), Thompson (1991a, 1991b), Young (1991), and Rohwer et al. (1992) based on apparent homologies of molts and plumages among and within these species, and (B) revised names suggested by Thompson and Leu (this paper) for the sequence of molts and plumages in these species based on a re-evaluation of molt and plumage homologies within and among species of *Passerina* and related taxa.

age that is similar in color to that of adult females. In the fall, one to three months after completion of the previous molt, they undergo a second molt in which they replace all of their body plumage, all juvenal retrices, and some juvenal outer primaries and inner secondaries. In winter and spring, birds replace some to all of their body plumage during a third molt called first prealternate molt (Fig. 1, Rohwer 1986, Thompson 1991a, Young 1991).

HOW TO USE THE HUMPHREY-PARKES SYSTEM TO NAME MOLTS AND PLUMAGES

If the sequence of molts and plumages of a bird is known, how does one correctly use the H-P system to name these molts and plumages? The key is to identify molt and plumage homologies among age classes within the same species as well as among closely related species. First, one must

determine the first and subsequent plumage "cycles" of the species of interest. 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. Having accomplished this, molt and plumage homologies may be determined and names assigned according to the following guidelines. (1) Molts held in common between the first and later plumage cycles can be homologized by comparing the timing and extent of molt, and the color change resulting from each molt in a given cycle (e.g., the first cycle) to those of molts of other cycles (e.g., second or later cycles) of the same species as well as to cycles in related species. (2) If there is one molt per cycle, it is called a prebasic molt that gives rise to a basic plumage. If there are two molts per cycle, one is a prebasic molt and the other a prealternate molt. These give rise to a

basic and alternate plumage, respectively. If one molt is complete and the other is incomplete, as is most common in passerines, then the complete molt usually is the prebasic molt and the incomplete molt is the prealternate molt. This, however, is only an empirical guide; names should always be assigned based on homology. If there are three molts per cycle, as in the first cycle of *Passerina*, then there must be a presupplemental molt in addition to the prebasic and prealternate molts. If three molts occur in a plumage cycle of a species but only two molts occur in other cycles of the same species or in cycles of related species, then the presupplemental molt must be the one molt that is not homologous to either of the two molts that occur in other cycles of the same species or in cycles of related species (Humphrey and Parkes 1959).

INCORRECT USE OF THE HUMPHREY-PARKES SYSTEM TO ASSIGN NAMES TO MOLTS AND PLUMAGES IN *PASSERINA*

Following the above logic of the H-P system, Rohwer et al. (1992) explained that they named the first molt in young *Passerina* the first prebasic molt (Fig. 1) "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." They named the second molt the presupplemental molt (Fig. 1) for three reasons. "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" (Rohwer et al. 1992).

We believe that the reasons given by Rohwer et al. (1992) to justify their nomenclatural scheme were incorrect. Except for *Passerina* and a few other genera (Willoughby 1986; Thompson, unpubl. data, discussed below), young birds of all known passerine species have only one molt of pennaceous feathers during the summer and fall after hatching. Ornithologists who use the H-P

system universally have held that this first and only molt out of juvenal body plumage into a partially or completely new plumage is homologous to definitive prebasic molt and, therefore, have called it first prebasic molt. Rohwer et al. (1992) correctly noted that in most passerine species other than *Passerina* spp., this first and only summer/fall molt replaces body feathers but not flight feathers (e.g., Ginn and Melville 1983, Pyle et al. 1987, Svensson 1992). However, they overlooked the fact that in passerines with only one summer/fall molt, the timing of this molt and the color change resulting from it coincide very closely with the timing and color change of the definitive prebasic molt in the large majority of species (Fig. 2) (Dwight 1900a; Forbush 1927, 1929; Roberts 1955; Pyle et al. 1987 and references therein). In contrast, in young Lazuli and Painted Buntings, but not Indigo Buntings, the timing of their second molt is more similar to that of the definitive prebasic molt than is the timing of their first molt (Fig. 3). We believe that the later timing of the second molt in young Indigo Buntings relative to that of definitive prebasic molt in adult Indigo Buntings must represent a derived condition among *Passerina*. We agree with Rohwer (1986) that selection caused by intraspecific competition on the wintering grounds favored the ability of subadult males to signal their competitive ability on the wintering ground; we further suggest that this selection resulted in a delay in the timing of the second molt in young Indigo Buntings until later in the year compared to other *Passerina*.

Rohwer et al. (1992) also noted that the second molt in *Passerina* involves replacement of outer but not inner primaries. They then imply that this is unique in passerines and that, as a result, this molt cannot be homologized to molts in other passerines. Thus, it should be named a presupplemental molt. However, replacement of outer but not inner remiges by young birds during their first summer and fall also occurs in all other species of *Passerina* as well as in all species of *Guiraca* and *Cyanocompsa* which belong to the same subfamily (Cardinalinae) as *Passerina*. Further, in North America alone, young birds of at least five other species in emberizinae, a subfamily of the family Emberizidae to which *Passerina* belongs, and at least five non-emberizid species also replace outer but not inner primaries during their first fall (Table 1). Many species outside of North America also exhibit this molt pat-

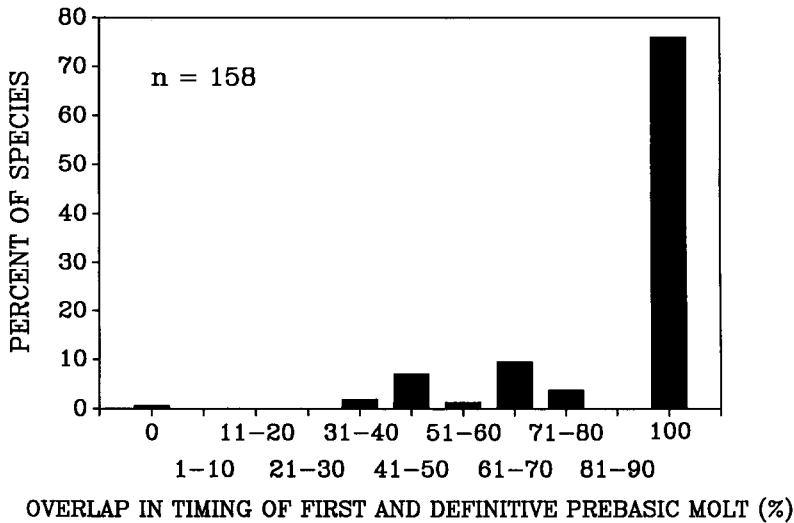


FIGURE 2. Overlap in timing of first prebasic and definitive prebasic molt in species in which first prebasic molt replaces body feathers only. Percent overlap was calculated as the number of days during which both first prebasic and definitive prebasic molt occur divided by the total number of days during which the first prebasic molt occurs. This underestimates the percent overlap in species in which the first prebasic molt overlaps the entire duration of the definitive prebasic molt but begins before and/or ends later than the definitive prebasic molt, e.g., Black Phoebes, *Sayornis nigricans*, Crissal Thrashers, *Toxostoma dorsale*, American Tree Sparrow, *Spizella arborea*, and Clay-colored Sparrows, *S. pallida*. Data regarding relative timing of first and definitive prebasic molt in each species were summarized from Pyle et al. (1987).

tern, e.g., *Elaenia* spp. (M. Traylor, pers. comm.), many *Lanius* shrikes (Phillips 1974), Sardinian Warblers, *Sylvia melanocephala*, Cirl Buntings, *Emberiza cirrus*, Greenfinches, *Carduelis chloris*, European Goldfinches, *C. carduelis*, Siskins, *C. spinus*, Red Crossbills, *Loxia curvirostra* (Winkler and Jenni 1987), Linnets, *Acanthis cannabina*, and Serins, *Serinus serinus* (Mester and Prunte 1982).

In Indigo Buntings, the second molt in young males results in a plumage that matches the moderately conspicuous definitive basic plumage of adult males, rather than the brown plumage worn by all females and by young males after their first molt. The similarity in plumage color between the second plumage of young male Indigo Buntings and the definitive basic plumage of adult males strongly suggests, contrary to Rohwer et al. (1992), that the second molt is homologous with the definitive prebasic molt and, therefore, should be renamed the first prebasic molt. This argument applies to the sequence of molts and plumages in Lazuli Buntings as well (Young 1991). In contrast, the second molt in young male Painted Buntings results in a plumage that is completely female-like in color and very similar

in color to the plumage that preceded it, i.e., Painted Buntings exhibit extreme delayed plumage maturation. Unlike Indigo and Lazuli Buntings in which the change in plumage color during this molt indicates the homology of the molt, the lack of change in plumage color resulting from this molt in young male Painted Buntings does not help clarify the homology of this molt.

EVIDENCE FROM OTHER SPECIES

We recently discovered that all *Cardinalis* spp., *Cyanocompsa* spp., Varied Buntings, *Passerina versicolor*, Orange-breasted Buntings, *P. leclancherii*, Rose-bellied Buntings, *P. rositae*, Blue Grosbeaks, *Guiraca caerulea*, Phainopeplas, *Phainopepla nitens*, and Yellow-breasted Chats, *Icteria virens*, exhibit the same sequence of molts and plumages as the *Passerina* species discussed above (Thompson and Leu, in press; Thompson, Leu and Dunn, unpubl. data). Cassin's Sparrows, *Aimophila cassinii*, and Bachman's Sparrows, *A. aestivalis*, also exhibit this sequence of molts and plumages (Willoughby 1986, Rohwer et al. 1992). For each of these species, data regarding the timing and extent of the first two molts of young

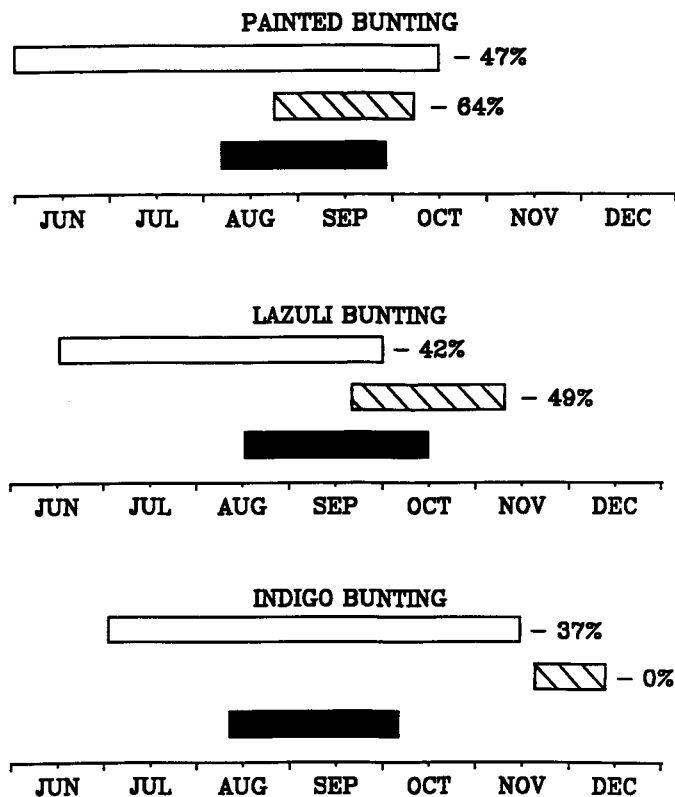


FIGURE 3. Relative timing of the first and second molts of young Indigo, *Passerina cyanea*, Lazuli, *P. amoena*, and Painted, *P. ciris*, with definitive prebasic molt in adults. Percent overlap was measured as the number of days during which first (or second) molt and definitive prebasic molt both occur divided by the total number of days on which only the first (or second) molt occurs. Data regarding timing of molts were obtained for Indigo Buntings from Emlen (1967), Johnston and Downer (1968), Rohwer (1986), and Payne (1992), for Lazuli Buntings from Young (1991), and for Painted Buntings from Thompson (1991a, 1991b). The duration of the second molt in Indigo and Painted Buntings and definitive prebasic molt in Indigo, Painted and Orange-breasted Buntings, *P. leclancherii*, was estimated from regression equations in Rohwer (1986), Young (1991), Thompson (1991a) and Thompson and Leu (in press) that were obtained by regression day of year on molt score (Pimm 1976). Open bars indicate the timing of the first molt after hatching; cross-hatched bars indicate the timing of the second molt after hatching; filled bars indicate the timing of definitive prebasic molt.

birds, and the color change resulting from each of these molts are presented below. These data support our contention that the second molt is homologous to the definitive prebasic molt and, therefore, that the second molt is the first prebasic molt rather than a presupplemental molt.

Timing of first and second molt. In most of the above species for which we have data, the timing of the second molt coincides much more closely with the timing of definitive prebasic molt than does the timing of the first molt (Fig. 4), thus suggesting that the second molt, and not the first molt, is homologous to the definitive prebasic molt.

Extent of first and second molts. As in the *Pas-*

serina discussed above, all of these species replace most or all of their juvenal body feathers (except greater primary and, sometimes, secondary coverts) during their first molt. All of these species also replace all rectrices and most to all of their new (second) body plumage during their second molt. However, the extent of replacement of remiges during the second molt varies both within and among species. This variation within and among species shows that the replacement of outer primaries and inner secondaries (and retention of inner primaries and outer secondaries) is not as unique as thought by Rohwer et al. (1992), but rather represents a special case of a more general pattern of remigial molt in car-

TABLE 1. Species of North American passerines (other than species in the subfamily Cardinalinae and that are not known to exhibit a presupplemental molt) in which young birds replace outer (distal) but not inner (proximal) primaries during a molt in the summer or fall after hatching.

Family	Species	Source
Remizidae	Verdins, <i>Auriparus flaviceps</i>	Taylor 1970, Austin and Rea 1971
Troglodytidae	Cactus Wrens, <i>Campylorhynchus</i>	Selander 1964
Laniidae	Loggerhead Shrike, <i>Lanius ludovicianus</i>	Miller 1928, 1931
Virconidae	White-eyed Vireo, <i>Vireo griseus</i>	George 1973, Lloyd-Evans 1983, Thompson 1973, Thompson, unpubl. data
Emberizidae	Rufous-winged Sparrow, <i>Aimophila carpalis</i>	Phillips 1951, Wolf 1977
Emberizidae	Rufous-crowned Sparrow, <i>Aimophila ruficeps</i> ¹	Wolf 1977
Emberizidae	Field Sparrow, <i>Spizella pusilla</i>	Willoughby 1989, 1992a
Emberizidae	Chipping Sparrow, <i>Spizella passerina</i>	Willoughby 1989, 1992a
Emberizidae	Lark Bunting, <i>Calamospiza melanocorys</i>	Roberts 1936
Fringillidae	House Finch, <i>Carpodacus mexicanus</i> ¹	Michener and Michener 1940, Stangel 1985

¹ Some individuals may replace all primaries.

dinaline finches and other passerine taxa. Yellow-breasted Chats and Varied, Orange-breasted and Rose-bellied Buntings, like other *Passerina* buntings, replace all body feathers, all rectrices, and typically the outer four to six primaries and inner three to five secondaries (Dwight 1899; Phillips 1974; Thompson and Leu, in press, unpubl. data). Blue Grosbeaks and *Cyanocompsa* spp. molt similarly but often replace more or rarely, all remiges (Thompson, Leu and Dunn, unpubl. data). Cardinals and Phainopeplas also molt similarly, but with two notable exceptions. First, primary and secondary (S1–S6) molt always begins at P1 and S1, respectively, with the result that juvenal outer primaries and inner secondaries (not including S7–S9) are retained by individuals that do not complete primary and/or secondary molt. This contrasts with all of the above species that begin remigial molt in the middle of the primaries and secondaries and always replace all outer primaries and inner secondaries. Second, the extent of flight feather molt is highly variable. Many individuals undergo a complete molt, the same as do adults. Most other individuals replace most of their flight feathers, although some individuals replace only a few or none. Bachman's and Cassin's Sparrows are similar to Cardinals and Phainopeplas in that they begin primary and secondary molt at P1 and S1, respectively. However, they differ from all of the species above in that they always undergo a complete molt, the same as do adults.

Change in plumage color resulting from first and second molt. Adult Yellow-breasted Chats,

Cassin's Sparrows and Bachman's Sparrows are both sexually and seasonally monomorphic. During both the first and second molt, young Yellow-breasted Chats grow plumages that are identical to those of adults. In Bachman's and Cassin's Sparrows, young birds grow a plumage during their first molt that differs from that of adults; their breast plumage is spotted rather than unmarked as in adults. However, during their second molt, they grow a plumage that is indistinguishable from that of adults in definitive plumage.

During their first molt, young Varied, Rose-bellied and Orange-breasted Buntings, Blue Grosbeaks, Phainopeplas, all *Cyanocompsa* spp., and all *Cardinalis* spp., replace most or all of their female-like juvenal plumage with a plumage that also is female-like in color. Similarly, during the second molt, all of these species except *Cardinalis*, Phainopeplas and Orange-breasted Buntings replace all of their body plumage and some to all of their primaries (as well as all rectrices and some to all secondaries) with another plumage that again is female-like in color; that is, these species, like the *Passerina* species discussed above, exhibit extreme delayed plumage maturation. This lack of change in plumage color does not help indicate the homology of this molt.

In contrast, young male Northern Cardinals, *Cardinalis cardinalis*, and Phainopeplas grow plumage during their second molt that is nearly or completely indistinguishable from that of older males in definitive plumage (Miller 1933, Sutton 1935, Thompson and Walsberg 1993). In

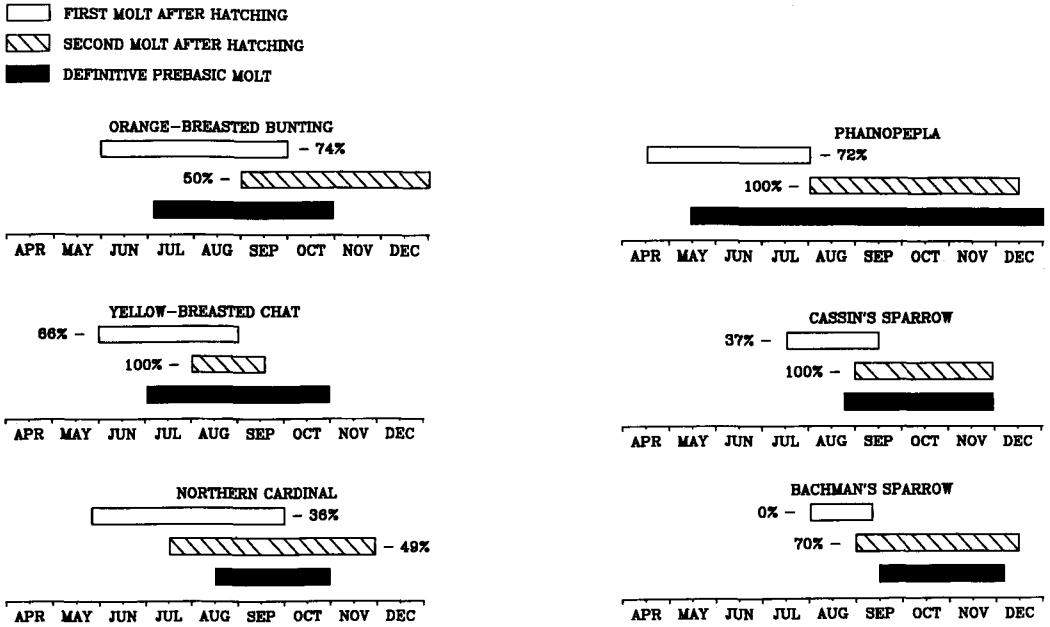


FIGURE 4. Relative timing of the first and second molts of young birds of six species previously unknown to undergo a presupplemental molt during the summer and fall after hatching. Data regarding the timing of molts were obtained for Orange-breasted Buntings, *Passerina leclancherii*, from Thompson and Leu (unpubl. manuscript), for Yellow-breasted Chats, *Icteria virens*, from Dwight (1899) and Phillips (1974), for Northern Cardinals, *Cardinalis cardinalis*, from Scott (1967), Blake (1971), Reese (1975), Wiseman (1977), and Yen (1989), for Phainopeplas, *Phainopepla nitens*, from Miller 1933 and Thompson and Walsberg (1993, unpubl. data), and for Cassin's, *Aimophila cassinii*, and Bachman's Sparrow, *A. aestivalis*, from Wolf (1977) and Willoughby (1986). Percent overlap in timing was calculated as described in Figure 3. The duration of the second molt in Yellow-breasted Chats was estimated from regression equations that were obtained by using unpublished data collected by Thompson and Leu to regress day of year on molt score following Pimm (1976).

addition, Orange-breasted Buntings grow a plumage that is intermediate between those of adult males and females (Thompson and Leu, in press).

IMPLICATIONS FOR HOMOLOGY OF MOLTS AND PLUMAGES

In most species discussed above in which young birds have two molts in the summer and fall after fledging, the second molt is much more similar to the definitive prebasic molt in its timing and extent, and in the change in plumage color resulting from it than is the first molt. This clearly indicates that the second molt is homologous to the definitive prebasic molt, and that the first molt is supplemental. Therefore, the second molt should be named first prebasic molt and the first molt should be named presupplemental (Fig. 1).

What are the implications of our data and the discussion above regarding birds in general, especially passerines? We speculate, for two rea-

sons, that the occurrence of a rapid body molt shortly after fledging followed shortly thereafter by a second molt, as described above, is probably widespread and common among passerines, but has been overlooked.

Until recently, all ornithological literature stated that young birds of all passerine species have only one molt in the summer and fall after fledging (e.g., Dwight 1900a; Forbush 1927, 1929; Ginn and Melville 1983). However, studies by Rohwer (1986), Willoughby (1986, 1992a), Young (1991) and Thompson and Leu (Thompson 1991a, 1991b; unpubl. data; Thompson and Walsberg 1993; Thompson and Leu, in press, unpubl. data) have shown that Phainopeplas and all of the emberizid species discussed above begin their first body molt within a few days after fledging, and complete it within a few weeks by the time their juvenal rectrices are full grown.

We believe that this first body molt was overlooked in these species, and probably continues

to be overlooked in many other species for two general reasons. First, young birds of such species are unlikely to be encountered during this molt because (1) they finish this molt within about a month after fledging, (2) they are relatively inactive for at least part of this period because they are fed by their parents, and (3) they are relatively immobile compared to older birds because their flight feathers are not completely grown and, therefore, they are poor flyers.

Second, because this molt occurs while juvenal rectrices and remiges are still growing, body plumage growing during this time has usually been assumed to be juvenal body plumage, rather than body plumage of a subsequent feather generation. This is illustrated by many descriptions of "juvenal" plumage which, in fact, are descriptions of the subsequent plumage; examples of such errors are discussed in Brewster (1878–1879) and Sutton (1935). Such errors are especially prone to occur in species like the emberizids discussed above because (1) the coloration of juvenal body plumage and of the subsequent generation that replaces it are very similar to one another, and (2) the second fall molt in young birds of these species may begin before completion of the previous molt at both the individual level and population level (e.g., in species with multiple clutches). As a result, the two molts often are perceived incorrectly to be one continuous molt, even by ornithologists who are knowledgeable about molt (e.g., Dwight 1900b).

That this molt was overlooked until recently in abundant, geographically widespread and generally well-studied species such as Indigo Buntings and Northern Cardinals is remarkable. More surprising is that this is true even in such species whose early molts and plumages have been studied in detail, sometimes independently by many investigators, e.g., five studies on "postjuvenal" molt in Northern Cardinals (Scott 1967, Blake 1971, Reese 1975, Wiseman 1977, Yen 1989). This demonstrates that such errors not only can happen, but have happened, even in species whose molts have been studied.

If our speculation is correct that the occurrence of a rapid body molt shortly after fledging is widespread among passerines but has been largely overlooked, then it may be that young passerines (and many nonpasserines) may follow one of two general molting strategies: (1) molt twice in the summer and fall after hatching, once immediately after fledging and a second time ap-

proximately synchronously with definitive prebasic molt in adults, or (2) molt once when adults undergo definitive prebasic molt. If so, a search for ecological differences between the groups of species that exhibit each molting strategy should help identify natural selection pressures that may have favored evolution of each of these strategies.

UTILITY OF THE HUMPHREY-PARKES SYSTEM

With the goal of providing ornithologists with a better way to study the evolution of molt and plumage succession in birds, Humphrey and Parkes (1959) developed an operationally practical, remarkably versatile and simple system for identifying molt and plumage homologies among age and sex classes within species as well as among related species. A consequence of their system for identifying molt and plumage homologies was a new system for naming molts and plumages. That their system is as useful today as it was 35 years ago is testament to their achievement and its contribution to ornithology.

Although the H-P system has been adopted explicitly by the American Ornithologist's Union and other national North American ornithological organizations, and is used widely by most North American ornithologists (Palmer 1962 and subsequent volumes, 1972; Pyle et al. 1987; Poole et al. 1992–1993 and subsequent volumes), many critics have claimed that it does not work as Humphrey and Parkes intended, much less in more general respects (e.g., Stresemann 1963; Amadon 1966; Willoughby 1986, 1992a, 1992b; Johnson 1993). Similarly, most ornithologists outside of North America do not use the H-P system (e.g., Snow 1970, Cramp et al. 1977 and subsequent volumes, Prater et al. 1977, Ginn and Melville 1983, Marchant and Higgins 1990 and subsequent volumes, del Hoyo et al. 1992, Svensson 1992, Jenni and Winkler 1994). We admit that some systems for naming molts and plumages other than Humphrey and Parkes may be suitable or necessary (e.g., when the sequence of molts and plumages of a species is not completely known) for addressing some kinds of questions. However, we also agree with Rohwer et al. (1992) that some of the criticism of the Humphrey-Parkes system has resulted because of confusion over the goal of the system (i.e., to address questions regarding the evolution of molt

and plumage sequences in birds) and how to apply it correctly.

This study clearly illustrates how the H-P system, if properly understood and applied, is a practical, flexible and powerful method for addressing questions regarding the evolution of molt and plumage sequences in birds. Indeed, because the H-P system relies on identifying molt and plumage homologies, unlike any other nomenclatural method (e.g., the "traditional" Dwight [1900a] method), the H-P system is the *only* existing method suitable for studying the evolution of molt and plumage sequences.

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LITERATURE CITED

- AMADON, D. 1966. Avian plumages and molts. *Condor* 68:263-278.
- AUSTIN, G. T., AND A. M. REA. 1971. Key to age and sex determination of Verdins. *Western Bird Bander* 46:41.
- BAKER, K. 1993. Identification guide to non-passerines. Guide 24. British Trust for Ornithology, Tring, U.K.
- BERTHOLD, P. 1985. Endogenous components of annual cycles of migration and moult, p. 922-929. *In* V. D. Ilyichev and V. M. Gavrilov [eds.], *Acta Congressus Internationalis Ornithologici*. Vol. 2. Nauka, Moscow, Russia.
- BLAKE, C. H. 1971. Primary molt in juvenile Cardinals. *Bird-Banding* 42:269-274.
- BRAUNE, B. M. 1987. Comparison of total mercury levels in relation to diet and molt for nine species of marine birds. *Arch. Environ. Contam. Toxicol.* 16:217-224.
- BREWSTER, W. 1878-1879. Descriptions of the first plumage in various species of North American birds. *Bull. Nuttall Ornithological Club* 3:15-23, 57-65, 115-128, 175-182; 4:39-46.
- BRODIN, A. 1993. Radio-ptilochronology—tracing radioactively labelled food in feathers. *Ornis Scand.* 24:167-173.
- BROWN, C. R. 1985. Energetic cost of moult in Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*). *J. Comp. Physiol. B* 155:515-520.
- BRUSH, A. 1990. Metabolism of carotenoid pigments in birds. *Fed. Am. Soc. Exp. Biol. J.* 4:2969-2977.
- BURTT, E. H., JR. 1986. An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithological Monogr.* 38. American Ornithologists' Union, Washington, DC.
- BUSSE, P. 1984. Key to sexing and aging of European passerines. *Beitr. Naturkd. Niedersachsens* 37.
- BUTCHER, G. S., AND S. ROHWER. 1989. The evolution of conspicuous and distinctive coloration for communication in birds, p. 51-108. *In* R. F. Johnston [ed.], *Current ornithology*. Vol. 6. Plenum Press, New York.
- CARNEY, S. M. 1984. Estimating the harvest, p. 256-259. *In* A. S. Hawkins, R. C. Hanson, H. K. Nelson, and H. M. Reeves [eds.], *Flyways: pioneering waterfowl management in North America*. U.S. Department of Interior, U.S. Fish and Wildlife Service, Washington, DC.
- CENA, K., J. A. CLARK, AND J. R. SPOTILA. 1986. Thermoregulation, p. 527-534. *In* J. Bereiter-Hahn, A. G. Matolsky, and K. S. Richards [eds.], *Biology of the integument. 2. Vertebrates*. Springer-Verlag, Berlin.
- CARNEY, S. M. 1992. Species, age and sex identification of ducks using wing plumage. U.S. Fish and Wildlife Service, Washington, DC.
- CHILGREN, J. D. 1978. Effects of photoperiod and temperature on postnocturnal molt in captive white-crowned sparrows. *Condor* 80:222-229.
- CRAMP, S., K.E.L. SIMMONS, I. J. FERGUSON-LEES, R. GILLMOR, P.A.D. HOLLOR, R. HUDSON, E. M. NICHOLSON, M. A. OGILVIE, P.J.S. OLNEY, K. H. VOOUS, AND J. WATTEL. 1977. *Handbook of the birds of Europe the Middle East and North Africa. The birds of the western palearctic. Volume 1. Ostrich to ducks*. Oxford University Press, New York.
- CRISSEY, W. F. 1984. Calculators and ouija boards, p. 259-271. *In* A. S. Hawkins, R. C. Hanson, H. K. Nelson, and H. M. Reeves [eds.], *Flyways: pioneering waterfowl management in North America*. U.S. Department of Interior, U.S. Fish and Wildlife Service, Washington, DC.
- DEL HOYO, J. A. ELLIOTT, AND J. SARGATAL. 1992. *Handbook of the birds of the world. Vol. 1. Lynx Edicions, Barcelona, Spain*.
- DORKA, V. 1981. Der Mausermodus der Flugfedern von *Corvus f. frugilegus* als Ausdruck oekologisch bedingter Anforderungen an den Flugapparat. *Diss. Abstr. Int. C. European Abstracts* 41(4):755.
- DWIGHT, J., JR. 1899. Sequence of plumages: illustrated by the Myrtle Warbler (*Dendroica coronata*) and the Yellow-breasted Chat (*Icteria virens*). *Auk* 16:217-220.
- DWIGHT, J., JR. 1900a. The sequence of plumages and moults of the passerine birds of New York. *Ann. N.Y. Acad. Sci.* 13:73-360.
- DWIGHT, J., JR. 1900b. The plumage and moults of the Indigo Bunting (*Passerina cyanea*). *Science* 11: 627-630.
- DWIGHT, J., JR. 1902. Plumage-cycles and the relation between plumages and moults. *Auk* 19:248-255.
- DWIGHT, J., JR. 1905. Sequence in moults and plumages, with an explanation of plumage cycles, p. 513-518. *In* R. B. Sharpe, E.J.O. Hartert and J.

- L. Bonhote [eds.], Proc. 4th Int. Ornithol. Congr. Dulau, London.
- EARNST, S. L. 1992. The timing of wing molt in Tundra Swans: energetic and non-energetic constraints. *Condor* 94:847-856.
- EMLEN, S. T. 1967. Migratory orientation in the Indigo Bunting, *Passerina cyanea*. *Auk* 84:309-342.
- EWINS, P. J. 1988. The timing of moult in Black Guillemots *Cepphus grylle* in Shetland. *Ring and Migr.* 9:5-10.
- FORBUSH, E. H. 1927. Birds of Massachusetts and other New England states. Vol. II. Land birds from bob-whites to grackles. Massachusetts Dept. of Agriculture, Boston.
- FORBUSH, E. H. 1929. Birds of Massachusetts and other New England states. Vol. III. Land birds from sparrows to thrushes. Massachusetts Dept. of Agriculture, Boston.
- FURNESS, R. W., AND A. E. BURGER. 1988. Effects of energy constraints on seabirds breeding at high latitudes, p. 1205-1217. *In Acta XIX Congressus Internationalis Ornithologici*. Vol. I. Univ. of Ottawa Press, Ottawa, ON.
- FURNESS, R. W., S. J. MUIRHEAD, AND M. WOODBURN. 1986. Using bird feathers to measure mercury in the environment: relationship between mercury content and moult. *Marine Pollution Bull.* 17:27-30.
- GASTON, A. J. 1981. Seasonal breeding, moulting and weight changes among birds of dry deciduous forest in North India. *J. Zool. (Lond.)* 194:219-243.
- GATES, R. J., D. F. CAITHAMER, T. C. TACHA, AND C. R. PAINE. 1993. The annual cycle of *Branta canadensis interior* in relation to nutrient reserve dynamics. *Condor* 95:680-693.
- GEORGE, W. G. 1973. Molt of juvenile White-eyed Vireos. *Wilson Bull.* 85:327-330.
- GINN, H. B., AND D. S. MELVILLE. 1983. Molt in birds. British Trust for Ornithology, Tring, U.K.
- GOODWIN, T. W. 1984. The biochemistry of the carotenoids. Vol. 2. Animals. 2nd ed. Chapman and Hall, London.
- GROSCOLAS, R., AND Y. CHEREL. 1992. How to molt while fasting in the cold: the metabolic and hormonal adaptations of Emperor and King Penguins. *Ornis Scand.* 23:328-334.
- GRUBB, T. C., JR. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. *Auk* 106:314-320.
- GRUBB, T. C., JR. 1992. Ptilochronology: a consideration of some empirical results and "assumptions" *Auk* 109:673-676.
- GRUBB, T. C., JR. In press a. On induced anabolism, induced caching and induced construction as unambiguous indices of nutritional condition. *Proc. West. Found. Vert. Zool.*
- GRUBB, T. C., JR. In press b. A workshop on ptilochronology, a new index of avian nutritional condition. *In R. Yosef and F. E. Lohrer [eds.], Proceedings of the International Shrike Symposium. Proc. West. Found. Vert. Zool.*
- GRUBB, T. C., JR., AND V. V. PRAVOSUDOV. 1994. Ptilochronology: follicle history fails to influence growth of an induced feather. *Condor* 96:214-217.
- HILL, G. 1992. Proximate basis of variation in carotenoid pigmentation in male House Finches. *Auk* 109:1-12 + frontispiece.
- HILL, G. 1993. The proximate basis of inter- and intra-population variation in female plumage coloration in the House Finch. *Can. J. Zool.* 71:619-627.
- HOHMAN, W. L., C. D. ANKNEY, AND D. H. GORDON. 1992. Ecology and management of postbreeding waterfowl, p. 128-189. *In B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], Ecology and management of breeding waterfowl. Univ. of Minnesota Press, Minneapolis, MN.*
- HUDON, J. 1994. Showiness, carotenoids, and captivity: a comment on Hill (1992). *Auk* 111:218-221.
- 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.
- JEHL, J. R., JR. 1990. Aspects of the molt migration, p. 102-113. *In E. Gwinner [ed.], Bird migration: physiology and ecophysiology. Springer-Verlag, Berlin, Germany.*
- JENNI, L., AND R. WINKLER. 1994. Molt and ageing in European passerines. Academic Press, New York.
- JOHN, T. M., M. VISWANATHAN, AND J. C. GEORGE. 1988. Immunocytochemical localization and seasonal changes in staining intensity of beta-endorphin-like immunoreactivity in the adenohipophysis of the migratory Canada Goose. *Cytobios* 56:179-193.
- JOHNSTON, N. K. 1993. Review of "Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proc. West. Found. Vertebr. Zool.* 4:247-286 by E. J. Willoughby" *In Wilson Bull.* 105:541-542.
- JOHNSTON, D. W., AND A. C. DOWNER. 1968. Migratory features of the Indigo Bunting in Jamaica and Florida. *Bird-banding* 39:277-293.
- KING, J. R. 1980. Energetics of avian moult, p. 312-317. *In R. Nöhning [ed.], Acta XVII Congressus Internationalis Ornithologici*. Vol. 1. Verlag der Deutschen Ornithologen-Gesellschaft, Berlin, Germany.
- KING, J. R., AND M. E. MURPHY. 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? *Amer. Zool.* 25:955-964.
- LLOYD-EVANS, T. L. 1983. Incomplete molt of juvenile White-eyed Vireos. *J. Field Ornithol.* 54:50-57.
- LOYE, J. E., AND M. ZUK. 1991. Bird-parasite interactions: ecology, evolution and behaviour. Oxford University Press, New York.
- MADSEN, R. M. 1967. Age determination of wildlife, a bibliography. U.S. Dept. of Interior, Department Library, Washington, DC.
- MARCHANT, S., AND P. J. HIGGINS. 1990. Handbook of Australian, New Zealand and Antarctic birds. Volume 1. Part A. Ratites to ducks. Part B. Pelicans to ducks. Oxford Univ. Press, New York.
- MESTER, H., AND W. PRÜNTE. 1982. Die "sektorale"

- postjuvenile Handschwingenmauser der Carduelinen in Südeuropa. *J. Ornithol.* 123:381-399.
- MICHENER, H., AND J. R. MICHENER. 1940. The molt of House Finches of the Pasadena region, California. *Condor* 42:140-153.
- MILLER, A. H. 1928. The molts of the Loggerhead Shrike *Lanius ludovicianus* Linnaeus. *Univ. Calif. Pubs. Zool.* 30:393-417.
- MILLER, A. H. 1931. Systematic revision and natural history of the American shrikes (*Lanius*). *Univ. Calif. Pubs. Zool.* 38:11-242.
- MILLER, A. H. 1933. Postjuvenile molt and appearance of sexual characters of plumage in *Phainopepla nitens*. *Univ. Calif. Pubs. Zool.* 38:425-446.
- MOORMAN, T. E., G. A. BALDASSARRE, T. J. HESS, JR. 1993. Carcass mass and nutrient dynamics of Mottled Ducks during remigial molt. *J. Wildl. Manage.* 57:224-228.
- MULVIHILL, R. S. 1993. Using wing molt to age passerines. *North American Bird Bander* 18:1-10.
- MURPHY, M. E. 1992. Ptilochronology: accuracy and reliability of the technique. *Auk* 109:676-680.
- MURPHY, M. E., AND J. R. KING. 1991a. Nutritional aspects of avian molt, p. 2186-2194. *In* B. D. Bell, R. O. Cossee, J.E.C. Flux, B. D. Heather, R. A. Hitchmough, C.J.R. Robertson, and M. J. Williams [eds.], *Acta XX Congressus Internationalis Ornithologici*. New Zealand Ornithological Congress Trust Board, Wellington, N.Z.
- MURPHY, M. E., AND J. R. KING. 1991b. Ptilochronology: a critical evaluation of assumptions and validity. *Auk* 108:695-704.
- MURPHY, M. E., AND J. R. KING. 1992. Energy and nutrient use during molt by White-crowned Sparrows *Zonotrichia leucophrys gambelii*. *Ornis Scand.* 23:304-313.
- MYHRE, G. 1980. Social status, external signals and caloric temperature in the captive Willow Grouse *Lagopus lagopus lagopus*. *Ornis Scand.* 11:77-80.
- NOORDHUIS, R. 1989. Patterns of primary moult: ecophysiological adaptations. *Limosa* 62:35-45.
- PALMER, R. S. 1962. Handbook of North American birds. Vol. 1. Loons through flamingos. Yale Univ. Press, New Haven, CT.
- PALMER, R. S. 1972. Patterns of molting, p. 65-102. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*. Vol. 2. Academic Press, New York, NY.
- PARTALI, V., S. LIAAEN-JENSEN, T. SLAGSVOLD, AND J. T. LIJFELD. 1987. Carotenoids in food chain studies—II. The food chain of *Parus* spp. monitored by carotenoid analysis. *Comp. Biochem. Physiol.* 87B:885-888.
- PAYNE, R. B. 1972. Mechanisms and control of molt, p. 104-155. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*. Vol. 2. Academic Press, New York.
- PAYNE, R. B. 1992. Indigo Bunting, p. 1-24. *In* A. Poole, P. Stettenheim, and F. Gill [eds.], *The birds of North America*, No. 4. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- PHILLIPS, A. R. 1951. The molts of the Rufous-winged Sparrow. *Wilson Bull.* 63:323-326.
- PHILLIPS, A. R. 1974. The first prebasic molt of the Yellow-breasted Chat. *Wilson Bull.* 86:12-15.
- PIERSMA, T. 1988. Breast atrophy and constraints on foraging during the flightless period of wing moulting Great Crested Grebes. *Ardea* 76:96-106.
- PIMM, S. 1976. Estimation of the duration of bird molt. *Condor* 78:550.
- POOLE, A., P. STETTENHEIM, AND F. GILL. 1992-1993. *The birds of North America*. Vol. 1, nos. 1-40. American Ornithologists' Union, Washington, DC, and Academy of Natural Sciences, Philadelphia, PA.
- PRATER, A. J., J. H. MARCHANT, AND J. VUORINEN. 1977. Guide to identification and ageing of holarctic waders. British Trust for Ornithology Guide 17. British Trust for Ornithology, Tring, U.K.
- 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.
- REESE, J. G. 1975. Fall remex and retrix molt in the Cardinal. *Bird-Banding* 46:305-310.
- REHDER, N. B., D. M. BIRD, AND P. C. LAGUE. 1982. Variations in blood packed cell volume of captive American Kestrels. *Comp. Biochem. Physiol. A* 72:105-109.
- ROBERTS, T. S. 1936. *The birds of Minnesota*. Second ed. Vol. 2. Univ. of Minnesota Press, Minneapolis, MN.
- ROBERTS, T. S. 1955. *A manual for the identification of the birds of Minnesota and neighboring states*. Univ. of Minnesota Press, Minneapolis, MN.
- 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 G. S. BUTCHER. 1988. Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. *Am. Nat.* 131:556-572.
- ROHWER, S., C. W. THOMPSON, AND B. E. YOUNG. 1992. Clarifying the Humphrey-Parkes molt and plumage terminology. *Condor* 94:297-300.
- ROUANET, J. L., AND H. BARRE. 1982. Les modifications metaboliques entrainees par le passage de la vie terrestre a la vie marine constituent elles un obstacle majeur au depart a l'eau des poussins non mues de manchot royal? *Comite National Francais des Recherches Antarctiques* 51:371-377.
- RUTTLEDGE, W. 1979. A study of wing moult and escape behaviour in the sky-lark. *Falconer* 7:190-195.
- RYMKEVICH, T. A., AND V. N. RYZHANOVSKY. 1987. To the moult in the passerine birds of the Polar Ural Mountains. *Ornitologiya* 22:84-95.
- SCOTT, D. M. 1967. Postjuvenile molt and determination of age of the Cardinal. *Bird-Banding* 38:37-51.
- SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. *Univ. Calif. Pubs. Zool.* 74.
- SMITH, J. P. 1982. Changes in blood levels of thyroid hormones in two species of passerine birds. *Condor* 84:160-167.
- SNOW, D. W. 1970. *A guide to moult in British birds*.

- British Trust for Ornithology Guide 11. British Trust for Ornithology, Tring, U.K.
- SPEARMAN, R.I.C. 1980. The avian skin in relation to surface ecology. *Proc. Roy. Soc. Edinburgh B* 79:57-74.
- SPEARMAN, R.I.C., AND J. A. HARDY. 1985. Integument, p. 1-56. *In* A. S. King and J. McLelland [eds.], *Form and function in birds*. Vol. 3. Academic Press, New York.
- STANGEL, P. W. 1985. Incomplete first prebasic molt of Massachusetts House Finches. *J. Field Ornithol.* 56:1-8.
- STOKKAN, C. A., P. J. SHARP, AND S. UNANDER. 1986. The annual cycle of the high-arctic Svalbard Ptarmigan (*Lagopus mutus hyperboreus*). *Gen. Comp. Endocrinol.* 61:446-451.
- STRESEMANN, E. 1963. The nomenclature of plumages and molts. *Auk* 80:1-8.
- SUTTON, G. M. 1935. The juvenal plumage and postjuvenal molt in several species of Michigan sparrows. *Cranbrook Institute of Science Bull.* no. 3.
- SVENSSON, L. 1992. Identification guide to European passerines. Rev. 4th ed. British Trust for Ornithology, Tring, UK.
- TABER, R. D. 1963. Criteria of age and sex, p. 119-149. *In* H. S. Mosby and O. H. Hewitt [eds.], *Wildlife investigational techniques*. 2nd ed. The Wildlife Society, Ann Arbor, MI.
- TAYLOR, W. K. 1970. Molts of the Verdin, *Auriparus flaviceps*. *Condor* 72:493-496.
- THOMPSON, C. F. 1973. Postjuvenal molt in the White-eyed Vireo. *Bird-Banding* 44:63-65.
- THOMPSON, C. W. 1991a. The sequence of molts and plumages in Painted Buntings and implications for the theories of delayed plumage maturation. *Condor* 93:209-235.
- THOMPSON, C. W. 1991b. Is the Painted Bunting actually two species? Problems determining species limits between allopatric populations. *Condor* 93:987-1000.
- THOMPSON, C. W. 1992. A key to aging and sexing Painted Buntings. *J. Field Ornithol.* 63:445-454.
- THOMPSON, C. W., AND M. LEU. *In press*. Molts and plumages of Orange-breasted Buntings: implications for theories of male and female delayed plumage maturation. *Auk*.
- THOMPSON, C. W., AND G. E. WALSBERG. 1993. Delayed plumage maturation in a subtropical frugivore is caused by dietary protein limitation. *American Zoologist* 32:97A.
- TUCKER, V. A. 1991. The effect of molting on the gliding performance of a Harris' Hawk (*Parabuteo unicinctus*). *Auk* 108:108-113.
- WALSBERG, G. E. 1981. The glossy appearance of a black bird: thermal effects. *J. Therm. Biol.* 5:185-188.
- WALSBERG, G. E. 1982. Coat color, solar heat gain, and visual conspicuousness in the Phainopepla. *Auk* 99:495-502.
- WALSBERG, G. E. 1983a. Avian ecological energetics, p. 161-220. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*. Vol. 7. Academic Press, New York, NY.
- WALSBERG, G. E. 1983b. Coat color and solar heat gain in animals. *BioScience* 33:88-91.
- WALSBERG, G. E. 1988a. Heat flow through avian plumages: the relative importance of conduction, convection, and radiation. *J. Therm. Biol.* 13:89-92.
- WALSBERG, G. E. 1988b. Solar heat gain in birds: consequences of plumage color, structure and optics, p. 2672-2680. *In* H. Ouellet [ed.], *Acta XIX Congressus Internationalis Ornithologici*. Univ. of Ottawa Press, Ottawa, ON.
- 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. 1989. The molts of Chipping Sparrows and Field Sparrows in Maryland. *Maryland Birdlife* 45:127-134.
- WILLOUGHBY, E. J. 1992a. Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proc. West. Found. Vertebr. Zool.* 4:247-286.
- WILLOUGHBY, E. J. 1992b. Incorrect use of the Humphrey-Parkes molt and plumage terminology for buntings of the genus *Passerina*. *Condor* 94:295-297.
- WINKLER, R., AND L. JENNI. 1987. Weitere Indizien für "sektorale" Handschwingenmauser bei jungen Singvögeln. *J. Ornithol.* 128:243-246.
- WISEMAN, A. J. 1977. Interrelation of variables in postjuvenal molt of Cardinals. *Bird-Banding* 48:206-223.
- WITHERBY, H. F., F.C.R. JOURDAIN, N. F. TICEHURST, AND B. W. TUCKER. 1943. *The handbook of British birds*. Vol. 1. H. F. & G. Witherby, London, U.K.
- WITSCHI, E. 1961. Sex and secondary sexual characters, p. 115-168. *In* A. J. Marshall [ed.], *Biology and comparative physiology of birds*. Vol. 2. Academic Press, New York, NY.
- WOLF, L. L. 1977. Species relationships in the avian genus *Aimophila*. *American Ornithologists' Union Monograph* no. 23.
- YEN, C.-W. 1989. A plumage study of the Cardinal (*Cardinalis cardinalis cardinalis*) of western Pennsylvania. *Bulletin of the National Museum of Natural Science, Taichung, Taiwan* no. 1:11-21.
- YOSEF, R., AND T. C. GRUBB, JR. 1992. Territory size influences nutritional condition in nonbreeding Loggerhead Shrikes (*Lanius ludovicianus*): a ptilochronology approach. *Conservation Biol.* 6:447-449.
- YOSEF, R., AND T. C. GRUBB, JR. *In press*. Ptilochronology: a potential biomarker for assessing territory quality and habitat suitability in shrikes. *In* R. Yosef and F. E. Lohrer [eds.], *Proceedings of the International Shrike Symposium*. *Proc. West. Found. Vert. Zool.*
- YOUNG, B. E. 1991. Annual molts and interruption of the fall migration for molting in Lazuli Buntings. *Condor* 93:236-250.
- ZUK, M. 1992. The role of parasites in sexual selection: current evidence and future directions. *Adv. Study Behav.* 21:39-68.