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MOLTS AND PLUMAGES OF ORANGE-BREASTED BUNTINGS (*PASSERINA LECLANCHERII*): IMPLICATIONS FOR THEORIES OF DELAYED PLUMAGE MATURATION

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ABSTRACT.—We document the sequence of molts and plumages in Orange-breasted Buntings (*Passerina leclancherii*), a nonmigratory passerine that is endemic to southwestern Mexico, and discuss implications of our results for theories of male and female delayed plumage maturation. This species has the same sequence of molts and plumages as all five other species of *Passerina*. However, in subadult (predefinitively plumaged) males and females, the intensity and extent of molts, as well as the plumage color (definitive malelike versus definitive femalelike) resulting from these molts, differ in many respects from other *Passerina*. The most significant difference is that female Orange-breasted Buntings exhibit delayed plumage maturation. For males and females, our results strongly support winter- and summer-status-signaling hypotheses for the evolution of delayed plumage maturation, and are inconsistent with winter- and summer-cryptic hypotheses, the female-mimicry hypothesis and the juvenile-mimicry hypothesis. Received 16 December 1993, accepted 12 May 1994.

MALES OF MANY SPECIES of birds do not reach maturity in plumage color or other secondary sexual characters such as bill, leg or iris color for months to years after reaching sexual ma-

turity (e.g. Skutch 1954, 1960, 1967, 1969, Snow 1982, Goodwin 1986, Rohwer and Butcher 1988, Thompson 1991a). In contrast, females of only a few species are known to exhibit delayed maturation of such characters (e.g. Stutchbury and Robertson 1987a, b, Mountjoy and Robertson 1988, Morton 1990, Peterson 1991a, b). Many investigators have proposed and tested hypoth-

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← **FRONTISPICE.** Orange-breasted Buntings (*Passerina leclancherii*). Top row (left to right) shows dorsal view of males collected in: (a) nonbreeding season in definitive basic plumage (DMNH 26943); (b and d) breeding season in definitive alternate plumage (USNM 185036 and MCZ 328421, respectively); (c) breeding season in first alternate plumage (LSUMZ 13993). Bottom row (left to right) shows ventral view of breeding-season birds: (e) subadult male in first alternate plumage (LSUMZ 13993); (f) adult male in definitive alternate plumage (MCZ 328421); (g) subadult female in first alternate plumage (LSUMZ 49451); (h) adult female in definitive alternate plumage (MLZ 54994).



TABLE 1. Sequence of molts and plumages in Orange-breasted Buntings (sexes combined).

Age at molting (months)	Molt ^a	Extent of molt	Resulting plumage ^a
0.5-3.0	Presupplemental (3, 4 ^b)	All body plumage (no flight feathers, greater primary and secondary coverts)	Supplemental (0, 0)
2-6	First prebasic (7, 8)	All body plumage, rectrices, P4-P9, S6-S9	First basic (55, 24)
6-11	First prealternate (13, 8)	Partial body molt, limited mainly to head	First alternate (6, 4)
12-17	Definitive prebasic (20, 11)	All body and flight feathers	Definitive basic (161, 78)
20-22	Definitive prealternate (4, 11)	Partial body molt, limited mainly to head	Definitive alternate ^c

^a Number of males and females examined, respectively, in parentheses.

^b Two specimens of unknown sex also examined.

^c Because definitive prealternate molt is very limited in extent and feathers grown during this molt are identical in color to those they replace, it is not possible to reliably distinguish nonmolting birds in definitive alternate plumage from those birds in definitive basic plumage.

eses for the evolution and maintenance of delayed plumage maturation (for reviews, see Rohwer et al. 1980, Rohwer and Butcher 1988, Thompson 1991a). These studies significantly advanced our understanding of natural and sexual selection pressures that favor evolution of different age-, sex-, and season-specific plumage color patterns and their ontogenies in various avian taxa. However, phylogenetic relationships and sequences of molts and plumages in these taxa are poorly known because few systematic studies, including ones employing molecular techniques, and few quantitative molt studies have been done on these taxa. Until we fill these gaps in our knowledge, the most basic assumptions underlying studies on the adaptive significance of plumage coloration cannot be evaluated.

The six species of the emberizine genus *Passerina* probably are a monophyletic group (Hellack and Schnell 1977, Tamplin et al. 1993), and all of these species exhibit delayed plumage maturation. The sequence of molts and plumages of Indigo, Lazuli, and Painted Buntings (*P. cyanea*, *P. amoena*, and *P. ciris*, respectively) were documented by Rohwer (1986), Young (1991) and Thompson (1991a, b, 1992), respectively. These studies indicated that all three species exhibit the same sequence of molts and plumages. However, the three differ markedly in the timing, location (breeding ground, wintering ground, or migratory stopover site) and extent of certain molts, and in the degree of change in plumage color resulting from each molt.

We currently are determining the sequence of molts and plumages in the three remaining

Passerina species—The Orange-breasted or Leclancher's Bunting (*P. leclancherii*), the Rose-bellied or Rosita's Bunting (*P. rositae*), and the Varied Bunting (*P. versicolor*). Our goal is to determine the evolutionary origin and adaptive significance of molt and plumage patterns in *Passerina* and its close relatives by correlating similarities and differences in these molt and plumage patterns with an independently derived molecular phylogeny of these taxa (J. Klicka, A. Fry, R. M. Zink, and C. W. Thompson unpubl. 1995 abstract). In this paper, we report the sequence of molts and plumages in Orange-breasted Buntings, a species endemic to southwestern Mexico; it breeds from May through July and is not known to migrate (Sharpe 1888, Ridgway 1901, Hellmayr 1938, Friedmann et al. 1957, Schaldach 1963, Alvarez del Toro 1971, AOU 1983, Escalante 1988, Binford 1989, Thompson and Leu unpubl. manuscript). We also discuss the implications of our results for theories of delayed plumage maturation.

MATERIALS AND METHODS

The data for this study were collected from: (1) 418 study skins that were loaned to us by 31 institutions (see Acknowledgments for names and acronyms of institutions); and (2) from 11 live specimens that were mist netted and examined in Oaxaca and Chiapas, Mexico in May 1993. Sample sizes of specimens in each molt and plumage are given in Table 1.

Molt and plumage terminology.—Between hatching and the beginning of their first potential breeding season when young *Passerina* buntings are about 10 months of age, they undergo three molts (described

below), not including their first (prejuvinal) molt, which replaces natal down with juvenal plumage. Rohwer (1986), Thompson (1991a, b), Young (1991), and Rohwer et al. (1992) followed the terminology of Humphrey and Parkes (1959) and named these molts first prebasic, presupplemental, and first prealternate in that order. Subsequent studies of molting sequences of other species in which we have discovered similar molting patterns indicate that the second molt (previously named presupplemental molt) is homologous to definitive prebasic molt, and that the first molt is a presupplemental molt (i.e. it is not homologous to any molt in subsequent molt cycles; Thompson and Leu 1994). As a result, in this paper we reversed the names of the first two molts (i.e. second molt is named first prebasic molt and first molt is named the presupplemental molt; for brief explanation of how to apply the Humphrey and Parkes system to naming molts and plumages, see Thompson and Leu 1994).

Determination of molt sequence, plumage sequence, and age.—All specimens were ordered in a linear array by day of year numbered from 1 (1 January) through 365 (31 December); no specimens were collected on 29 February. To determine the sequence of molts and plumages, we began by identifying birds in juvenal plumage. In passerines, nestlings fledge when most or all of their remiges and rectrices are incompletely grown and sheathed at their bases. Such fledglings have pennaceous body feathers that appear very fluffy and loose in structure because these feathers have a lower density of barbs, and interlocking barbules on these barbs, compared to feathers that replace them in subsequent plumages (Dwight 1900, Chandler 1916, Lucas and Stettenheim 1972); also, many fledglings still possess some natal down feathers at this stage of development. This first pennaceous feather generation must be the juvenal plumage. To identify birds in presupplemental molt, we examined all specimens possessing any juvenal body plumage. All such specimens with partly or completely grown body feathers that differed in feather structure and/or color from juvenal plumage must be in presupplemental molt (i.e. growing feathers must be supplemental feathers). We identified subsequent molts and plumages by the same criteria, as well as by differences in feather wear between growing feathers and full grown feathers of previous feather generations, and by differences in the extent and timing of molt.

Identification of sex.—Unless the reproductive condition of a specimen is indicated on its label (and even then, the incorrect sex may be indicated; e.g. females occasionally are misidentified as males because preparators misidentify female adrenal glands as testes), it is not possible to verify the sex indicated on its label by a criterion that is independent of plumage color. By determining the molt and plumage sequence (described above), we were able to determine reliable aging (i.e. plumage class) criteria. Having done so, we then identified discrete plumage criteria by

which the sex of specimens in each plumage class (except juvenal plumage) may be identified with greater than 99% certainty (Table 2). We did this by comparing and identifying differences in plumage color between sexes within each plumage class (e.g. all birds in supplemental plumage), examining only those specimens whose sex was verified by data on their reproductive condition (presence, size or condition of gonads, seminal vesicles, oviduct, cloacal protuberance, or brood patch). In turn, we then used these criteria to verify the sex of specimens lacking data on their reproductive condition. This study and previous studies of species with delayed plumage maturation that were based on study skins have shown that only 1 to 2% of specimens indicate the incorrect sex, even in species like Painted Buntings in which males in predefinitive plumages usually are nearly indistinguishable in plumage color from females (Thompson 1991a).

Scoring molt.—We examined specimens under a 2× magnifying lamp equipped with an incandescent 100-watt bulb. We determined the extent of body molt by lifting the feathers with watchmaker's forceps at 5 to 10 points on each of six body regions (as defined by Rohwer 1986): (1) forehead and crown; (2) back; (3) face (auricular region, ocular region, and lores); (4) chin and throat; (5) breast; and (6) belly. The intensity of body molt in each region was scored by visually estimating the percentage of growing (sheathed) feathers to the nearest 20% as follows: (0) no molt; (15) 10–20%; (30) 21–40%; (50) 41–60%; (70) 61–80%; and (90) greater than 80%. In addition, specimens with less than 10% body molt were assigned molt scores as follows: (2) 1–3% molt; (5) 4–6%; and (8) 7–9%. To avoid quantifying adventitious molt, we assigned a molt score only to those birds with at least five molting feathers in a single body region. If two or more molting feathers were found in each of at least two body regions, we assumed this to be molt. We calculated the mean percentage of body feathers in molt by taking the average of the six body regions.

For birds in first and definitive prebasic flight-feather molt, we assigned each flight feather a molt score between 0 and 1 as follows: (0) old (previous generation); (0.1) missing or less than 10% full grown; (0.2) 11–20% full grown; . . . ; (0.9) 91–100% full grown and sheathed at base of rachis; (1.0) full grown and unsheathed. During the first prebasic molt, Orange-breasted Buntings replace all rectrices, four to eight primaries, and three to six secondaries. Most often birds replace primaries (P) 4 through 9 and secondaries (S) 6 through 9. In order to measure remigial molt of all birds on the same numerical scale, birds that initiated primary molt at P3 or P2 (molt never began at P1) received a score of 0 for each of these feathers. Similarly, birds that began primary molt distal to P4 received a score of 1.0 for each primary between (and including) P4 and the primary at which molt was initiated. Likewise, birds that started secondary molt distal to S6 received a score of 0 for

each secondary replaced between and including S1 through S5. Birds that replaced their "tertials" (S7-S9), but not S6, received a molt score of 1.0 for S6.

The maximum flight-feather molt score for birds in first prebasic molt is 32.0 (12 primaries, 8 secondaries, and 12 rectrices). For the definitive prebasic molt, during which all flight feathers are replaced, the maximum flight-feather molt score is 48.0 (18 primaries, 18 secondaries, and 12 rectrices).

Feather wear.—The definitive prealternate molt (described below) is very limited in extent and, thus, is not a major cause of change in plumage color between winter and summer. However, males in definitive basic and definitive alternate plumage change plumage color (aspect) significantly from winter to summer due to feather wear. After completion of definitive prebasic molt in the fall, the forehead, crown and back of males are mostly Parrot Green (capitalized names of colors follow Smithe 1975). Subsequently, the forehead and crown become increasingly Lime Green, and the back Cerulean Blue as the tips of these feathers wear off and expose the underlying Lime Green (forehead and crown) and Cerulean Blue (back) bases of these feathers (see Frontispiece). Other body areas change color little or not at all due to feather wear. We assigned each male in definitive basic plumage a feather-wear score according to a ranked scale from least to most feather wear. To score back color, we first selected a set of seven male specimens in definitive basic and definitive alternate plumage with back color that varied from Parrot Green (fresh and unworn) to Cerulean Blue (old and worn). All non-molting males in definitive basic and definitive alternate plumage then were compared to these reference specimens and assigned a back score between 1 (least worn) and 7 (most worn). Specimens intermediate between two reference specimens received a score halfway in between (e.g. a 5.5 if between 5 and 6). The following were used as reference specimens: score 1 (DMNH 26943, least wear; Frontispiece, top left); 2 (LSUMZ 27614); 3 (USNM 531628); 4 (USNM 185036; Frontispiece, top and second from left); 5 (MLZ 43581); 6 (MLZ 43416); and 7 (MLZ 37825).

Statistics.—All statistical tests were performed using SYSTAT (Wilkinson 1990). We used the 0.05 level of significance in all tests. The mean duration of flight-feather molt for individuals was calculated by regressing Julian date (e.g. 1 January = 1, 31 December = 365) on molt score. The more intuitive approach of regressing molt score on Julian date indicates mean duration of molt for an entire population, but not for individuals (Pimm 1976).

RESULTS

The sequence of molts and plumages of Orange-breasted Buntings is identical to that of all other *Passerina* species. However, the intensity, extent and timing of molts and the plum-

age color (definitive malelike versus definitive femalelike) resulting from molts in this sequence varies in many respects from other *Passerina* species (Rohwer 1986, Thompson 1991a, Young 1991, Thompson and Leu unpubl. data).

Juvenal plumage.—We did not examine any specimens wearing exclusively juvenal plumage (i.e. that had not already begun presupplemental molt; Table 3). Juvenal plumage differs from all subsequent plumages in that it is uniformly Drab (brown) and lax in appearance due to the differences in feather structure described above. Sexes are identical in color in juvenal plumage (Table 2).

Presupplemental molt.—Birds typically replace all body plumage except greater primary and secondary coverts during this molt. We observed molting contour feathers in all areas of the body of specimens in this molt (Table 4). Furthermore, only 3 of 15 specimens that had completed this molt (i.e. specimens in supplemental plumage or first prebasic molt) retained any juvenal body plumage (UNAM-INST P011479, P013213, and P013222).

This molt begins when all juvenal flight feathers are incompletely grown and sheathed. Rectrices often are less than one-half grown at the onset of this molt (e.g. WFVZ 3076, LSUMZ 49467). This molt begins at the latest within a few days after fledging. At the population level, this molt begins as early as the first part of June and ends as late as the end of September (Table 3, Fig. 1).

Supplemental plumage.—Both sexes exhibit delayed plumage maturation in supplemental plumage. The breast band of males in this plumage is much less distinct and less Spectrum Orange than that of males in definitive plumage. Similarly, the breast and belly of females in this plumage is Trogon Yellow with longitudinal Olive Green (color chip 260) streaks (anterior-posterior) in contrast to females in definitive plumage (described below) that have Spectrum Yellow breasts with no streaking (Frontispiece, Table 2).

Birds in supplemental plumage (e.g. female MLZ 54724, male FMNH 102722) can be distinguished readily from all subsequent plumage classes by retention of all juvenal greater secondary coverts (brown), occasionally some additional juvenal body plumage (discussed above), and all juvenal flight feathers (edged light brown or light green; Table 2).

First prebasic molt.—Typically, all body plum-

TABLE 2. Color of plumages in Orange-breasted Buntings.*

Plumage	Forehead and crown	Nape and back	Sides of head	Chin and throat	Breast	Belly
Juvenal Supplemental	Drab (brown) Olive Green	Drab (brown) Olive Green	Drab (brown) Olive Green	Drab (brown) Cream Color	Drab (brown) ♂ Spectrum Yellow with diffuse/incomplete Spectrum Orange band; ♀ Trogon Yellow with heavy Olive Green streaks	Cream Color ♂ Trogon Yellow; ♀ Trogon Yellow with light Olive Green streaks
First basic and first alternate	♂ Parrot Green; ♀ Olive Green	♂ Parrot Green; ♀ Olive Green	♂ Cerulean Blue; ♀ Olive Green	Spectrum Yellow	Same as previous plumage	Same as previous plumage
Definitive basic	Parrot Green	♂ Parrot Green; ♀ Olive Green	♂ Cerulean Blue; ♀ Olive Green to dull Cerulean Blue	Same as previous plumage	♂ Spectrum Yellow with broad/complete Spectrum Orange breast band; ♀ Spectrum Yellow with some Spectrum Orange	Spectrum Yellow
Definitive alternate	♂ Lime Green (by wear); ♀ same as previous plumage	♂ Cerulean Blue (by wear); ♀ same as previous plumage	Same as previous plumage	Same as previous plumage	Same as previous plumage	Same as previous plumage

* Capitalized color names follow Smithie (1975). He used same name for as many as three different color chips. Thus, accurate use of Smithie (1975) requires identification of his color chips by their unique number: (chip 67) Cerulean Blue, (54) Cream Color, (27) Drab, (159) Lime Green, (46) Olive Green, (160 in ♂♂; 260 in ♀♀) Parrot Green, (17) Spectrum Orange, (55) Spectrum Yellow, and (153) Trogon Yellow.

TABLE 3. Temporal frequency distribution of pre-supplemental and first prebasic molt in Orange-breasted Buntings (sexes combined).

Month	No. examined	Percentage (no.) of specimens in	
		Presupplemental molt	First prebasic molt
June	2	100.0 (2)	0.0 (0)
July	1	100.0 (1)	0.0 (0)
August	6	66.7 (4)	33.3 (2)
September	9	22.2 (2)	77.8 (7)
October	2	0.0 (0)	100.0 (2)
November	11	0.0 (0)	27.3 (3)
December	12	0.0 (0)	8.3 (1)

age except some or all of the greater primary coverts, all rectrices, the outer six primaries, and the inner four secondaries is replaced in this molt (Tables 1, 4 and 5). At the population level, the end of presupplemental overlaps the beginning of first prebasic molt in August and September (Fig. 1, Table 3). This raises the possibility that what we call the first prebasic molt is not a discrete molt, but simply a continuation of presupplemental molt in which the timing of onset of flight-feather molt is delayed relative to that of body molt. This is not the case for three reasons.

First, feathers on the auriculars, head, breast and back of males and on the throat of females that are replaced at the same time as flight feathers differ in color from those that are replaced in the same body areas during the previous episode of body molt when flight-feather molt is absent. These differences in plumage color in all body areas also indicate that this second episode of body molt typically involves the replacement of all body plumage.

Second, in most species of birds, including other *Passerina*, body plumage is usually replaced during molt in a specific order (i.e. it begins in one body region, such as the ventral

pterylae, and progresses in sequential fashion through other pterylae until body molt is completed). Thus, if the body molt that occurs simultaneously with flight-feather molt is a continuation of presupplemental molt, then body molt should occur on different areas of the body before flight-feather molt than it does during flight-feather molt. However, we found growing body feathers in all regions of the body both before and during flight-feather molt (e.g. 64, 64 and 73% of specimens in flight-feather molt had growing body feathers on their back, breast and belly, and head, respectively; Table 4).

Third, all specimens in the latter stages of flight-feather molt or that had completed flight-feather molt had replaced their greater secondary coverts and often some greater primary coverts. These are groups of feathers that are never replaced during body molt before the onset of flight-feather molt.

All specimens in first basic plumage had replaced all of their rectrices indicating that juvenal rectrices are rarely, if ever, retained during first prebasic molt. In addition, as in all other *Passerina* species, rectrices are replaced synchronously. Primary molt most frequently begins at P4 (range is P2-P7) and progresses outward to the most distal primary, P9. All specimens always replaced all of their "tertials" (S7-S9), usually beginning with S8, followed by S7 and S9 in seemingly random order, and then usually by S6, S5 and S6, or S4-S6 beginning with the outermost secondary. Analysis of frequencies indicates that males replace the same number of secondaries, but fewer primaries, during this molt than do females (Table 5; primaries, G-test for independence with Williams' correction [Sokal and Rohlf 1981:710], $G_{adj} = 13.75$, $df = 5$, $P = 0.017$; secondaries, $G_{adj} = 0.905$, $df = 3$, $P = 0.824$). In addition, there is a positive correlation in males and females between the number of primaries and secondaries replaced

TABLE 4. Percentage of Orange-breasted Bunting specimens molting in each of six body regions during different molts (sexes combined).

Body region	Presupplemental (n = 9)	First prebasic (n = 15)	First prealternate (n = 21)	Definitive prebasic (n = 31)	Definitive prealternate (n = 15)
Chin and throat	44.4	38.5	36.8	59.3	50.0
Breast	88.9	53.8	21.1	74.1	25.0
Belly	44.4	33.8	26.3	66.7	25.0
Face	11.1	30.8	63.2	59.3	33.3
Forehead, crown, and nape	77.8	38.5	36.8	51.9	25.0
Back	77.8	76.9	52.6	74.1	33.3

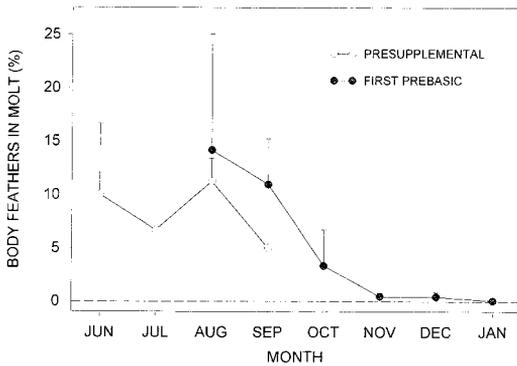


Fig. 1. Timing and intensity of presupplemental and first prebasic body molt in Orange-breasted Buntings (sexes combined). Mean and 1 SE indicated.

during this molt (males, $r = 0.375$, $df = 50$, $P < 0.005$; females, $r = 0.806$, $df = 27$, $P < 0.001$).

This molt occurs from August through December (Figs. 1 and 2, Table 3) with a peak in intensity of body molt in September when 78% of all birds of the year were in molt. Regression of day of year on flight-feather molt score (Pimm 1976) indicates that completion of flight feather molt requires approximately 50 days beginning, on average, on 2 September and ending on 27 October (Fig. 2).

First basic plumage.—Birds in this plumage can be identified by the presence of new rectrices, inner secondaries, outer primaries, and often some outer greater primary coverts that have blue outer edges. These new flight feathers and coverts are darker in color than retained juvenal remiges and inner greater primary coverts, which are more worn and uniformly brown in color. Males are identical to definitive females, but can be distinguished from first basic females by the presence of Cerulean Blue auriculars and a Spectrum Orange breast band (Frontispiece, Table 2). In both sexes, plumage color is at least a little brighter in first basic plumage than in sup-

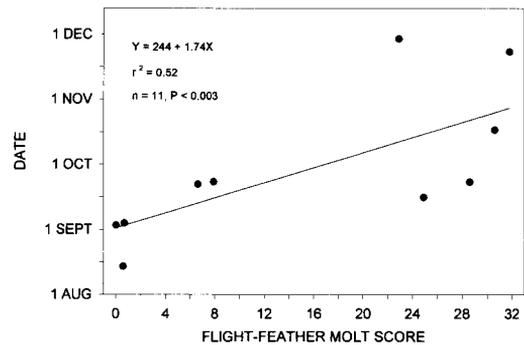


Fig. 2. Linear regression of collection date (Julian date) against flight-feather molt score for Orange-breasted Buntings (sexes combined) in first prebasic molt. Y-axis labeled with months of year, but numerically represents Julian date. Thus, in regression equation, Y expressed as Julian date (e.g. 1 January = 1, 31 December = 365), and X is molt score.

plemental plumage. Females acquire a Spectrum Yellow chin and throat, and males acquire a Parrot Green forehead, crown and back, a Spectrum Yellow chin, throat and belly, and Cerulean Blue auriculars. However, as in supplemental plumage, both sexes exhibit delayed plumage maturation in first basic plumage. Females maintain a light Trogon Yellow breast with Olive Green (color chip 260) streaks and males lack the distinct bright Spectrum Orange breast band and bright Cerulean Blue back of males in definitive plumage and, thus, are similar to females in definitive plumage (Frontispiece, Table 2).

First prealternate molt.—In both males and females, feathers grown during this molt differ in color in some body regions from those grown during first prebasic molt. Back feathers of males in first alternate plumage have barbs that are blue basally and green distally whereas the back feathers of males in first basic plumage are entirely green (i.e. have no blue color). Similarly,

TABLE 5. Primaries and secondaries replaced in Orange-breasted Buntings during first prebasic molt.

Primaries replaced	Percentage of		Secondaries replaced	Percentage of	
	Males (n = 58)	Females (n = 28)		Males (n = 54)	Females (n = 29)
P7-P9	1.7	0.0	S7-S9	13.0	20.7
P6-P9	1.7	3.6	S6-S9	61.1	58.6
P5-P9	24.1	17.9	S5-S9	18.5	17.2
P4-P9	55.2	46.4	S4-S9	5.6	3.4
P3-P9	17.2	21.4	S3-S9	0.0	0.0
P2-P9	0.0	10.7	S2-S9	1.9	0.0

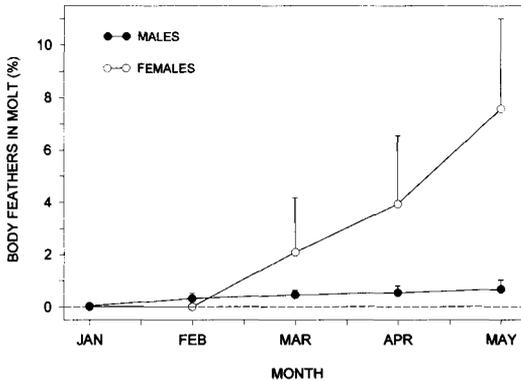


Fig. 3. Timing and intensity of first prealternate body molt in Orange-breasted Buntings. Mean and 1 SE indicated.

females grow breast feathers during this molt that are solely Spectrum Yellow in color; they do not grow Olive Green (color chip 260) streaked breast feathers that characterize first basic plumage (Table 2).

This is a low-intensity partial body molt during which some head and, less frequently, some body feathers are replaced (Table 4). We observed nearly symmetrical replacement of tertials (S7 and S8 on right wing, and S8 and S9 on left) in one male specimen (MLZ 28656), but in no females. Although the large majority of these birds that we examined had some growing or full-grown first alternate plumage (Table 4), some specimens collected in June and July did not appear to have any first alternate plumage, thus suggesting that a small proportion of these birds may not undergo any first prealternate molt.

This molt is more intense in females than in males (Fig. 3; two-way ANOVA, $F = 3.936$, $df = 4$ and 164 , $P < 0.005$). In May when this molt is most intense in both sexes, females had an average of 7.6% molting body feathers, whereas males had an average of only 0.7% (Fig. 3). A similar difference exists between older males and females (discussed below).

The first prealternate molt begins as early as January, but occurs mostly from March through May (Table 6, Fig. 3). No birds were found in this molt in June or later.

First alternate plumage.—In first alternate plumage, as in supplemental and first basic plumages, both sexes exhibit delayed plumage maturation. Even though some males and females acquire feathers in first prealternate molt

TABLE 6. Percent (number examined) of Orange-breasted Buntings in first prealternate molt.

Month	Males	Females
January	10.0 (10)	0.0 (2)
February	27.3 (11)	0.0 (8)
March	75.0 (4)	50.0 (2)
April	14.3 (7)	100.0 (2)
May	35.7 (14)	83.3 (6)

that are similar in color to definitive plumage of males and females, respectively, the extent and intensity of first prealternate molt is so limited that the summer (first alternate) plumage of these birds is significantly less brightly colored than that of older birds in definitive alternate plumage. As in first basic plumage, males in this plumage can be distinguished from females by the presence of Cerulean Blue auriculars and a Spectrum Orange breast band (Frontispiece, Table 2).

Definitive prebasic molt.—All body plumage, remiges and rectrices are replaced during this molt. Because Orange-breasted Buntings occupy physically abrasive habitats, especially thorn scrub, they usually have very worn plumage in late summer (July and August) prior to definitive prebasic molt. Therefore, new feathers growing during this molt can be detected easily. Flight-feather molt begins approximately simultaneously with the innermost primary (P1) and the tertials, the latter beginning with S8. Molt of the remaining secondaries (S1–S6) begins at S1 at about the same time that P3, P4 or P5 is dropped. Primaries are replaced from the innermost (P1) distally to the outermost (P9); secondaries are replaced from the outermost (S1) proximally to S6. All juvenal (brown) greater primary coverts are replaced during this molt with blue-edged greater primary coverts.

This molt typically occurs from July through November, although some birds may not complete their body molt until mid-January (e.g. female DMNH 26942; male MLZ 25144; Figs. 4 and 5, Table 7). Comparison of linear regressions of day of year on flight-feather molt score of birds undergoing their first definitive prebasic molt versus older birds undergoing their second or later definitive prebasic molt indicates that younger birds begin molting in June, about one month earlier, on average, than do older birds (Y -intercept, $n = 5$, $t = 7.47$, $P < 0.001$). Comparison of linear regressions of day of year on flight-feather molt score for older

TABLE 7. Percent (number examined) of Orange-breasted Buntings in definitive prebasic molt.

Month	Males	Females
July	2.2 (45)	7.1 (14)
August	46.2 (13)	66.7 (3)
September	60.0 (10)	100.0 (4)
October	66.7 (3)	100.0 (1)
November	15.4 (13)	50.0 (4)
December	33.3 (6)	0.0 (1)
January	3.1 (1)	6.7 (15)

males versus older females indicates that the timing and rate of second or later definitive prebasic molt does not differ between sexes (Y -intercept, $t = 0.593$, $P = 0.56$; slope, $t = 0.406$, $P = 0.69$). Molt typically begins on 16 August and is completed on 21 October (Fig. 5).

Definitive basic plumage.—As mentioned above, back feathers of males in definitive basic plumage have bright Parrot Green tips and Cerulean Blue bases. As a result, after completion of definitive prebasic molt in winter, males have bright Parrot Green backs. As winter and spring progress and breeding season approaches, males acquire increasingly Cerulean Blue backs as the green tips of their back feathers wear off, thereby exposing the blue bases (see Frontispiece). This is reflected by a significant positive correlation between day of year and back color (Spearman rank correlation, $r_s = 0.543$, $P = 0.001$; Fig. 6).

Males can be distinguished from females in definitive basic plumage by their broad Spectrum Orange breast band and, usually, by their bright Cerulean Blue backs (Frontispiece, Table 2). In birds in this plumage, all of their remiges except P9 and all greater primary coverts have

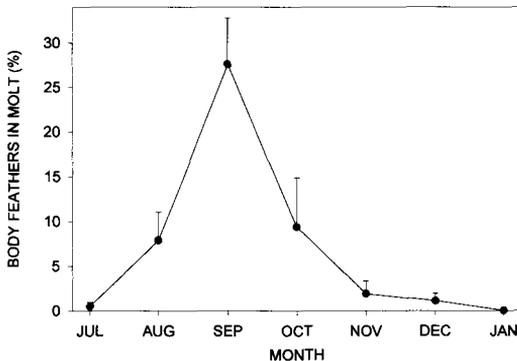


Fig. 4. Timing and intensity of definitive prebasic body molt in Orange-breasted Buntings (sexes combined). Mean and 1 SE indicated.

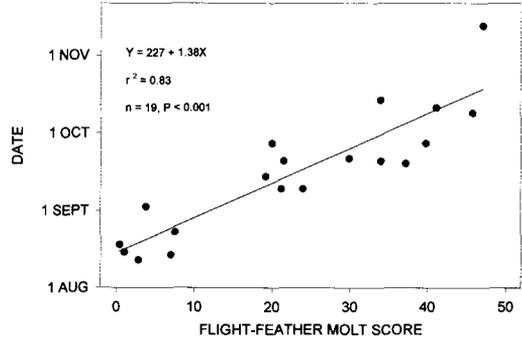


Fig. 5. Linear regression of collection date (Julian date) against flight-feather molt score for Orange-breasted Buntings (sexes combined) in first prebasic molt. Y -axis labeled with months of year, but numerically represents Julian date. Thus, in regression equation, Y expressed as Julian date (e.g. 1 January = 1, 31 December = 365), and X is molt score.

blue edges. Thus, birds in this plumage can be distinguished from birds in predefinitive plumages that have retained (uniformly brown) juvenal inner primaries, outer secondaries and some to all greater primary coverts.

Definitive prealternate molt.—Definitive basic and alternate plumages are identical. Body feathers grown during this molt are identical in color to those grown during definitive prebasic molt. Thus, the extent, frequency and in-

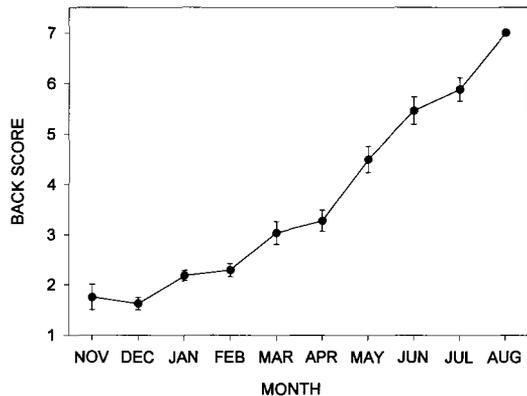


Fig. 6. Change in color of back feathers with date of definitive male Orange-breasted Buntings that results from feather wear from time definitive prebasic molt is completed (typically late October) until onset of following definitive prebasic molt in mid-August. Back score 1 is bright green (Frontispiece, top left), and back score 7 is bright blue (Frontispiece, top and second from left). For each month (e.g. 1–31 January), mean \pm 1 SE indicated.

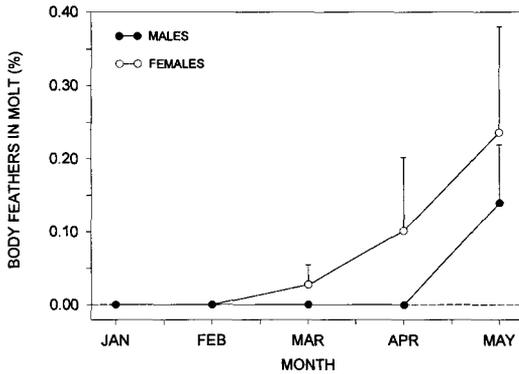


Fig. 7. Timing and intensity of definitive prealternate molt in Orange-breasted Buntings. Mean and 1 SE indicated.

tensity of this molt are difficult to determine. The occurrence of definitive prealternate molt can be detected only by observing growing definitive alternate feathers and sometimes in males by differences in wear between worn definitive basic and newly grown definitive alternate back feathers. We found feathers growing in all body regions (Table 4).

The definitive prealternate molt is a limited body molt that occurs in March, April and May. Like first prealternate molt, this molt seems to be more intense in females than in males; however, this difference is not significant (two-way ANOVA, $F = 2.62$, $df = 3$ and 95 , $P = 0.111$; Fig. 7, Table 8).

Definitive alternate plumage.—This plumage is identical to definitive basic plumage in both males and females.

DISCUSSION

Comparison with other Passerina.—Using *Passerina* as a model to address general questions regarding evolution of molts, plumages, and seasonal color change in birds, our main goal was to clarify the adaptive significance of their sequence of molts, including the timing and extent of each, and corresponding changes in plumage color resulting from each molt.

Feather wear.—Feather wear often is invoked as the main selective factor that regulates the frequency and extent of molts. This almost certainly is true in some species that live in physically abrasive environments (e.g. certain emberizid sparrows [Greenlaw and Rising 1994, Willoughby 1992] and some desert alaudids

TABLE 8. Percent (number examined) of Orange-breasted Buntings in definitive prealternate molt.

Month	Males	Females
January	0.0 (32)	0.0 (15)
February	0.0 (24)	0.0 (15)
March	0.0 (20)	22.2 (9)
April	0.0 (15)	28.6 (7)
May	16.7 (24)	30.4 (23)

[Willoughby 1971]), and some species that migrate exceptionally long distances (e.g. Franklin's Gull, *Larus pipixcan* [Burger and Gochfeld 1994], and some tyrannids and hirundinids [summarized by Pyle et al. 1987]). However, it is unlikely that feather wear has acted as a significant selection pressure to influence either the number (i.e. frequency) of molts or the extent of molts in either young or adult Orange-breasted Buntings. (Feather wear has played a major role, however, in the evolution of feather color and structure, and the mechanism [i.e. wear versus molt] by which *Passerina* species undergo seasonal changes in plumage color.) Two lines of evidence support this conclusion: (1) Drastic differences exist among species of *Passerina* in the physical abrasiveness of the environments in which they live, their geographic distributions, and their migratory strategies. However, all *Passerina* exhibit the same sequence of molts and a similar extent of replacement within each molt (i.e. ecological differences among *Passerina* species are not correlated with differences in molt and plumage sequence, which might suggest that feather wear significantly influenced the sequence or extent of molts in this genus). (2) Except at the end of breeding season, birds never exhibit extensive feather wear; thus, feathers grown during all molts except definitive prebasic molt, replace relatively new and unworn feathers of the previous plumage. This is especially true of the replacement of supplemental plumage by first basic plumage only days to weeks after completion of presupplemental molt. This suggests that first prebasic, presupplemental, and first prealternate molts occur primarily to cause seasonal changes in plumage color.

Seasonal change in plumage color.—The plumage color of Orange-breasted Buntings in winter and summer, and the mechanisms responsible for their changes in plumage color between seasons are an interesting mixture of those exhibited by other *Passerina* (Rohwer 1986,

Thompson 1991a, Young 1991): (1) Orange-breasted Buntings differ from all other *Passerina* except the Rose-bellied Bunting (Thompson and Leu unpubl. data) in that young females wear predefinitive (i.e. subadult sensu Rohwer et al. 1980) plumages in their first winter and during the following summer (breeding season) that are more cryptic in color than female definitive plumages. (2) As in Indigo and Lazuli buntings, subadult males grow definitive (hereafter adult) malelike plumage during their first prebasic molt in fall and during their first prealternate molt the following spring. In contrast, subadult male Painted and Varied buntings grow almost exclusively adult femalelike plumage during these molts. (3) As in Painted and Varied buntings, subadult males undergo a very limited prealternate body molt, and do not change color significantly from winter to summer. In contrast, subadult male Lazuli and Indigo buntings change color dramatically from winter to summer by feather wear and an extensive first prealternate spring molt, respectively. (4) Like adult male Painted and Lazuli buntings, adult males undergo a very limited spring molt in which they grow plumage that is identical in color to their previous winter plumage. In contrast, adult male Indigo Buntings undergo an extensive spring molt in which they grow an exclusively bright blue plumage that is much brighter and more conspicuous than their previous winter plumage. (5) Subadult and adult male Painted and Orange-breasted buntings do not change plumage color between winter and summer except for adult male Orange-breasted Buntings that change back color by feather wear (Frontispiece). In contrast, adult male Indigo Buntings change dramatically from winter to summer by an extensive body molt, and adult male Lazuli and Varied buntings do so mostly through feather wear.

Delayed somatic maturation.—Perhaps our most interesting finding is that delayed plumage maturation occurs in female as well as male Orange-breasted Buntings. This is a surprising result because delayed maturation of plumage or other secondary sex characters is fairly common and has been well studied in males (for reviews, see Rohwer and Butcher 1988, Butcher and Rohwer 1989, Thompson 1991a), but is much less common and less studied in females. No published summary or review exists of the occurrence of delayed somatic maturation in birds; however, a cursory search of a few major references (e.g. Diamond 1972, Schodde 1982, Grant

1986, Lawton and Lawton 1986, Forshaw and Cooper 1990) indicates that delayed somatic maturation occurs in males of more than 200 species and 30 families of passerine birds, but in females of only 26 species (including *Passerina*) and 8 families of passerine birds (Table 9). This raises a question: Why is delayed somatic maturation so rare in females and what can this tell us about the conditions that favor evolution of delayed somatic maturation?

Theories of delayed somatic maturation.—All theories for the evolution of delayed somatic maturation state that male and female subadult plumages evolve in response to either of two selection pressures: (1) intense intraspecific (and usually intrasexual) competition for a limiting resource; or (2) interspecific predation in which case the cryptic color of their subadult plumage presumably reduces their risk of predation. In the former case, subadult plumage reduces aggression directed toward competitively inferior subadults by more dominant conspecifics. In the latter case, the proximate mechanism by which subadult plumage color may elicit less aggression from conspecifics or attacks by predators than does adult plumage may be: winter or summer status signaling; crypsis; winter or summer female mimicry; or juvenile mimicry. These hypotheses and the predictions they imply are reviewed below.

The winter- and summer-status-signaling hypotheses (Rohwer 1975, 1977, 1978, 1982, 1985, Rohwer and Ewald 1981, Lyon and Montgomerie 1986, Montgomerie and Lyon 1986, Rohwer and Butcher 1988) state that plumage color functions intraspecifically to honestly signal dominance rank within social groups, conspicuous color being dominant to more cryptic color. Status signals also may function to indicate inherent cost-benefit asymmetries among group members (Parker 1974, Maynard Smith and Parker 1976, Ewald and Rohwer 1980). These two hypotheses predict that winter and/or summer plumage of subadults should reliably indicate their fighting ability. Since Orange-breasted Buntings fledge young as early as the first part of June and as late as early to mid-September, young birds vary greatly in relative age and, therefore, presumably in fighting ability during their first winter and the following breeding season. Thus, these hypotheses predict that the extent of adult malelike plumage acquired by subadult Orange-breasted Buntings as a result of molt in the fall and/or following spring should be correlated with fighting ability and,

TABLE 9. Species in which females exhibit delayed maturation of plumage or other secondary sex characters during their first winter and, in most cases, the following summer.*

Species	References
Monarchidae	
Buff-bellied Monarch, <i>Neolalage banksiana</i> (P)	Mayr 1933a, b
Hirundinidae	
Tree Swallow (P)	Hussell 1983, Stutchbury and Robertson 1987a, b, c
Corvidae	
Pinyon Jay, <i>Gymnorhinus cyanocephalus</i> (P)	Sutton 1967, Ligon 1971
Gray-breasted Jay, <i>Aphelocoma ultramarina</i> (B)	Pitelka 1945, 1951, Brown and Horvath 1989, Peterson 1991a, b
Unicolored Jay, <i>A. unicolor</i> (B)	Pitelka 1951, Goodwin 1986
Beechey's Jay, <i>Cyanocorax beecheii</i> (B)	Davis 1960, Hardy 1973
San Blas Jay, <i>C. sanblasianus</i> (I, B)	Davis 1960, Hardy 1973, Hardy and Raitt 1977, Goodwin 1986
Yucatan Jay, <i>C. yucatanicus</i> (B, COS)	Hardy 1973
Bushy-crested Jay, <i>C. melanocyaneus</i> (I, B)	Hardy 1973, Goodwin 1986
Motacillidae	
Pied Wagtail, <i>Motacilla alba varrellii</i> (P)	Cramp 1988
Yellow Wagtail, <i>M. flava</i> (P)	Cramp 1988
Bombycillidae	
Cedar Waxwing (P)	Yunick 1970, Mountjoy and Robertson 1988
Emberizidae	
Northern Parula, <i>Parula americana</i> (P)	Rappole 1983
Bay-breasted Warbler, <i>D. castanea</i> (P)	Rappole 1983
Chesnut-sided Warbler, <i>D. pensylvanica</i> (P)	Rappole 1983
Yellow Warbler, <i>D. petechia</i> (P)	Morton 1976
American Redstart, <i>Setophaga ruticilla</i> (P)	Morton 1990
Hooded Warbler, <i>Wilsonia citrina</i> (P)	Spellman et al. 1987
Wilson's Warbler, <i>W. pusilla</i> (P)	Rappole 1983
Kentucky Warbler, <i>Oporornis formosus</i> (P)	Rappole 1983
Yellow-breasted Chat, <i>Icteria virens</i> (P)	Rappole 1983
Rosita's Bunting, <i>Passerina rositae</i> (P)	Thompson and Leu unpubl. data
Orange-breasted Bunting, <i>P. leclancherii</i> (P)	Thompson and Leu, this study
Northern Oriole, <i>Icterus galbula</i> (P)	Rappole 1983
Yellow-rumped Caticue, <i>Cacicicus cela</i> (P)	Skutch 1954
Fringillidae	
Laysan Finch, <i>Telespyza cantans</i> (P)	Banks and Laybourne 1977

* Character exhibiting delayed maturation in color follows name of each species. Indicated as follows: (P) plumage; (B) bill; (I) iris; and (COS) circumorbital skin.

therefore, should vary considerably among subadults. In addition, the more conspicuous that subadult winter and/or summer plumage is, on average, relative to the plumage that preceded it, the stronger is the support for winter- and/or summer-status-signaling hypotheses, respectively.

The winter- and summer-cryptic hypotheses (Lack 1968, Selander 1965, 1972, Ewald and Rohwer 1980, Proctor-Gray and Holmes 1981, Rohwer et al. 1983, Rohwer 1986, Rohwer and Butcher 1988) propose that the relatively cryptic plumage of subadults reduces their conspicuousness to both predators and conspecifics. They

predict that subadult winter and summer plumages should be equally or more cryptic than the fall and winter plumages, respectively, that preceded them.

The winter-female-mimicry hypothesis (Brown and Brown 1988) proposes that, in species in which breeding males preferentially allow females access to resources, subadult males with adult femalelike plumage may mimic females to increase their access to resources in winter. Subadult males may exploit this relationship between adult males and females by wearing adult femalelike plumage that deceives other males into identifying and treating them

as females. For this hypothesis to be true, adult males must benefit, on average, from their differential behavior toward females; specifically, one must assume that: (1) reciprocal altruism (Trivers 1971) exists among adult males and females; or (2) that by doing so, adult males may increase their probability of pairing and/or mating with these females in the future.

Similarly, the summer-female-mimicry hypothesis (Rohwer et al. 1980, 1983, Rohwer 1983) proposes that adult males minimize aggression toward females during breeding season to facilitate pair bonding or extrapair copulations. It further argues that subadult males exploit this by behaving like females for a short time early in the breeding season. In migratory species, this is the time period immediately after spring arrival. By doing so, they are able to deceive adult males into perceiving them as females. In turn, this allows them to gain access to suitable breeding habitat for sufficient time to establish site dominance and, then, to unveil their sex by establishing and defending a breeding territory.

An alternative explanation for female mimicry is that selection favors "males to allow females access to food that may be channeled into the production of eggs and young in which males have genetic interest" (Brown 1984). As in winter female mimicry, subadult males may exploit this relationship between adult males and females by wearing adult femalelike plumage that deceives other males into identifying and treating them as adult females. For this hypothesis to be true, the same conditions must exist as for winter female mimicry.

The juvenile-mimicry hypothesis (Lawton and Lawton 1986, Foster 1987) proposes that: (1) juvenile rather than femalelike morphological and/or behavioral characters are retained by subadult males during their first winter and, in some species, the following summer; and (2) adults display less aggression toward subadults than toward adult females. Foster (1987) further asserted that retention of juvenilelike characters during the summer (breeding season) by sexually mature subadults deceitfully signals nonreproductive status, whereas Lawton and Lawton (1986, pers. comm.) maintained that retention of juvenilelike characters may either deceitfully signal age or honestly signal subordination.

Implications for female delayed somatic maturation.—Female delayed somatic maturation has

been studied in only five other species: Hooded Warblers (*Wilsonia citrina*; Morton 1990, Stutchbury 1994), Yellow Warblers (*Dendroica petechia*; Morton 1976), Tree Swallows (*Tachycineta bicolor*; Stutchbury and Robertson 1985, 1987a, b, Stutchbury and Rohwer 1990, Lozano and Handford 1995), Cedar Waxwings (*Bombocilla cedrorum*; Mountjoy and Robertson 1988), and Rose-bellied Buntings (Leu and Thompson unpubl. data). Ecological and life-history studies of these species suggest that subadult female plumage functions to signal: (1) status in winter in Yellow Warblers (Morton 1976); (2) status (Morton 1990) or reduce conspicuousness to predators or conspecific territory holders (Stutchbury 1994) in Hooded Warblers in winter; (3) sex and/or status in Tree Swallows (Lefelaar and Robertson 1985, Stutchbury and Robertson 1985, 1987a, b, Robertson et al. 1986, Lozano and Handford 1995); and (4) age (possibly correlated with quality) in Cedar Waxwings (Howell 1973, Mountjoy and Robertson 1988).

Both subadult and adult female Orange-breasted Buntings are more brightly colored than females of all other *Passerina*, *Cyanocompsa* and *Guiraca*; the latter two genera often are considered congeneric with *Passerina* (e.g. Paynter and Storer 1970). Females also exhibit delayed plumage maturation unlike any other cardinaline finch except Rose-bellied Buntings (Thompson and Leu unpubl. data). Their bright plumage color, including their similarity in color to adult males, suggests that their plumage color probably serves a status-signaling function of some kind. This view is corroborated by the color of feathers grown during first prebasic and first prealternate molt, and the changes in plumage color resulting from these molts. During first prebasic molt, females acquire auricular patches that are dull Parrot Green to dull Cerulean Blue, and breast and belly plumage that is Trogon Yellow with dark Olive Green (color chip 260) longitudinal streaks (see Frontispiece). This plumage is much more conspicuous and brightly colored than their preceding supplemental plumage. Similarly, in spring, females undergo a limited body molt during which they become still more brightly colored by replacing some of their streaked breast and belly plumage with additional Trogon Yellow breast and belly plumage. These findings support the predictions discussed above of the winter and summer-status-signaling hypotheses, but are inconsistent with those of the winter- and

TABLE 10. Theoretically possible changes in color of plumage or other secondary sex characters in species with delayed somatic maturation from summer to winter^a by young males and females born that year, and their implications for winter hypotheses for evolution of delayed somatic maturation. Observed changes in first-year male and female Orange-breasted Buntings are preceded by ♂ and ♀, respectively.

Changes that support (S), are consistent with (C) or are inconsistent with (I) the hypothesis.

Winter-status-signaling hypothesis

♂ ♀ More definitive malelike (S)
No change (C)
More definitive femalelike (I in ♂, S in ♀)

Winter-cryptic hypothesis

♂ ♀ More conspicuous (I)
No change (C)
Less conspicuous (S)

Winter-female-mimicry hypothesis^b

♂ More definitive malelike (I)
No change (C)
More definitive femalelike (S)

^a Change in plumage color from summer to winter may result from presupplemental molt, first prebasic molt, feather wear, or a combination thereof. Summer-status-signaling, summer-cryptic, summer-female-mimicry, juvenile-mimicry, and molt-constraints hypotheses make no predictions regarding changes in color from summer to winter.

^b Applies to males only.

summer-cryptic hypotheses and the juvenile-mimicry hypothesis (Tables 10 and 11).

Implications for male delayed somatic maturation.—Empirical studies to determine whether delayed plumage maturation is adaptive during the breeding or nonbreeding season have yielded support for both seasons, although the bulk of the evidence suggests that, in most species, delayed somatic maturation probably evolves, at least initially, as an adaptation to nonbreeding season (usually winter; Rohwer and Butcher 1988, Stutchbury and Rohwer unpubl. manuscript). Regardless of the season(s) during which subadult plumages may serve a signaling function (including intra- and interspecific crypsis), the proximate mechanism(s) by which subadult plumages reduce aggression or predation directed toward subadults is not well understood. The majority of studies suggest that subadult plumages are used to honestly signal status, age, or sex, and are not used for crypsis or female mimicry. However, female mimicry appears to operate in at least two species: (1) In Pied Flycatchers (*Ficedula hypoleuca*), some subadult males have relatively cryptic gray-and-white femalelike plumage, rather than conspicuous black-

TABLE 11. Theoretically possible changes in color of plumage or other secondary sex characters in species with delayed somatic maturation from winter to summer by subadult males and females born the previous summer, and their implications for hypotheses for evolution of delayed somatic maturation. Observed changes in first-year male and female Orange-breasted Buntings are preceded by ♂ and ♀, respectively.

Changes that support (S), are consistent with (C) or are inconsistent with (I) the hypothesis

Winter-status-signaling hypothesis

♂ ♀ More definitive malelike (C)
No change (C)
More definitive femalelike (S in ♂, C in ♀)

Winter-cryptic hypothesis

♂ ♀ More conspicuous (C)
No change (C)
Less conspicuous (I)

Winter-female-mimicry hypothesis^a

♂ More definitive malelike (C)
No change (C)
More definitive femalelike (I)

Summer-status-signaling hypothesis

♂ ♀ More definitive malelike (S)
No change (C^b, I^b in ♂)
More definitive femalelike (I)

Summer-cryptic hypothesis

♂ ♀ More conspicuous (I)
No change (C^c, I)
Less conspicuous (S)

Summer-female-mimicry hypothesis^b

♂ ♀ Less definitive femalelike (I)
No change (I^d, S^d)
More definitive femalelike (S)

Juvenile-mimicry hypothesis

♂ ♀ Less juvenilelike (I)
No change (S^e, I^e)
More juvenilelike (S)

Molt-constraints hypothesis

No predictions

^a Applies to males only.

^b No change in plumage color is consistent with this hypothesis only when subadult male winter plumage color is intermediate between that of males and females in definitive plumage, and is inconsistent with this hypothesis when subadult male winter plumage color is completely definitive femalelike, as occurs in Orange-breasted Buntings.

^c No change in plumage color is consistent with this hypothesis only if subadult winter plumage color is maximally cryptic, which is not the case in Orange-breasted Buntings.

^d No change in plumage color is inconsistent with this hypothesis only if subadult male winter plumage color is not completely definitive femalelike, and supports this hypothesis only if subadult male winter plumage color is completely definitive femalelike, as occurs in Orange-breasted Buntings.

^e No change in plumage color supports this hypothesis only if subadult male winter plumage color is completely juvenilelike, and is inconsistent with this hypothesis if subadult male winter plumage color is not completely juvenilelike, as occurs in Orange-breasted Buntings.

and-white plumage as in adult males, which deceives other males into treating them as females (Slagsvold and Saetre 1991). This result is especially compelling because Götmark (1992, 1993, 1995) demonstrated in a series of elegant experiments that subadult males with relatively cryptic (femalelike) plumage suffer higher rates of predation, contrary to predictions of the cryptic hypotheses, than do more conspicuous adult males. (2) In Painted Buntings, subadult males grow plumage during both first prebasic and first prealternate molt that is almost exclusively adult femalelike, rather than adult malelike, in color, thus supporting the predictions of the winter- and summer female-mimicry hypotheses (Tables 10 and 11).

In Orange-breasted Buntings, males acquire bright Cerulean Blue auricular patches and bright Spectrum Orange and Spectrum Yellow breast and belly plumage during the first prebasic molt. Similarly, in spring, males undergo a limited first prealternate body molt during which they become still more brightly colored by growing back feathers that have bright Cerulean Blue bases (unlike the Parrot Green bases of first basic feathers). These findings support the predictions discussed above of the winter- and summer-status-signaling hypotheses, but are inconsistent with those of the winter- and summer-cryptic and female-mimicry hypotheses, as well as the juvenile-mimicry hypotheses (Tables 10 and 11).

Molt constraints.—The molt-constraints hypothesis (Rohwer et al. 1983, Rohwer 1986, Rohwer and Butcher 1988) proposes that subadult males are unable to attain adult breeding plumage by their first potential breeding season because of an inability to acquire sufficient resources (fat or protein) for a late winter or spring molt. Cryptic plumages worn by subadult males during their first potential breeding season, therefore, are viewed as maladaptive. In addition, if subadult males do not replace all of their body plumage during a prebreeding molt in late winter or spring, their winter and summer plumages may not be functionally independent (i.e. it is not clear whether subadult plumages evolved as an adaptation to winter, but are retained in summer because of resource constraints in spring, or vice-versa). In such cases, no definite conclusions can be made regarding the season to which subadult male plumages are adapted.

This hypothesis makes no predictions re-

garding the color of plumage grown during predefinitive molts by subadults (Tables 10 and 11). However, it does predict that subadults should molt less extensively than adults during a late-winter or spring molt, and would be supported by this result. Conversely, a complete prebreeding body molt by subadults would be inconsistent with this hypothesis. Last, in species in which adult males and/or females do not change plumage color from winter to summer, it is possible that subadults may molt more extensively than adults of the same sex and still be physiologically constrained. How is this so? If molt is physiologically costly in such species, selection probably would favor little or no late-winter or spring molt in adults because such a molt would not result in any substantial change in their plumage color. However, a late-winter or spring molt in subadults probably would be favored by selection because it would cause a significant change in plumage aspect. Thus, in such species, subadults may exhibit a more extensive late-winter or spring molt than adults, yet still be unable to molt as extensively as would be optimal because of resource limitations. This result would be consistent with the molt-constraints hypothesis.

In Orange-breasted Buntings, the frequency and intensity of prealternate molt is greater in subadults than adults (Figs. 3 and 7, Tables 4, 6 and 8). However, as discussed above, because adult male and female Orange-breasted Buntings do not change plumage color from winter to summer, this result is consistent with the molt-constraints hypothesis, but neither supports nor refutes it.

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