

A PREVIOUSLY UNKNOWN PLUMAGE OF FIRST-YEAR INDIGO BUNTINGS AND THEORIES OF DELAYED PLUMAGE MATURATION

SIEVERT ROHWER

Burke Museum DB-10 and Department of Zoology, University of Washington, Seattle, Washington 98195 USA

ABSTRACT.—First-year, but not adult, Indigo Buntings (*Passerina cyanea*) have a previously unknown supplemental plumage. The presupplemental molt includes all of the rectrices, the outermost but not the innermost primaries, and, typically, the three innermost secondaries and all body feathers. In this molt, young females exchange one adult-femalelike plumage for another, while young males exchange an adult-femalelike plumage for one that matches that of adult males in winter. Thus, in their first year Indigo Buntings wear: first, the juvenile plumage, the body feathers of which begin replacement before the tail is fully grown; second, the first basic plumage, which in both sexes is entirely femalelike in coloration and includes the juvenile remiges and rectrices; third, the supplemental plumage, assumed either prior to fall migration (<10% of individuals) or on the wintering ground (>90% of individuals) and in which obvious sexual dichromatism is first achieved; and fourth, the first alternate plumage, acquired in a prolonged and often incomplete prealternate molt of body feathers that occurs during February, March, and April on the wintering ground and during the spring in the United States.

Because almost all of the femalelike first basic plumage of young males is lost in the presupplemental molt, this plumage almost certainly is an adaptation to conditions encountered either in the fall or early in the first winter. Furthermore, the ensuing supplemental plumage cannot be compromised by color requirements of the first breeding season because of the intervening prealternate molt; thus, the adult-malelike plumage produced by the presupplemental molt likely evolved to meet a change in signaling requirements that occurs in early winter. The signaling function of this plumage is unknown. Because this supplemental plumage of young males resembles the winter plumage of adult males and because all feathers grown by young males in their first prealternate molt resemble those of the adult male breeding plumage, the female mimicry hypothesis of Rohwer et al. (1980) is untenable for the subadult breeding plumage of yearling male Indigo Buntings. *Received 16 August 1984, accepted 5 October 1985.*

THEORIES of delayed plumage maturation for male passerines may be divided into sets of summer and winter adaptation hypotheses (Rohwer et al. 1983, Rohwer and Butcher unpubl.). Two hypotheses consider subadult plumages to be an adaptation to conditions of the first potential breeding season. The cryptic hypothesis (Lack 1954, Selander 1965) considers both the infrequency of breeding by subadults and their subdued appearance to be adaptive responses to the inferiority of subadults in competition with older males. The female mimicry hypothesis (Rohwer et al. 1980, Rohwer 1983) views failures by subadults to breed as maladaptive, and their femalelike plumage as an adaptation by which young males increase, through deception, the likelihood of acquiring female-worthy territories and of breeding in their first summer. Two other hypotheses consider subadult plumages as an

adaptation to conditions encountered in the first winter. The status signaling hypothesis (Rohwer 1975, Ketterson 1979, Rohwer and Ewald 1981) treats the subdued first winter plumage of young birds as a badge of subordination that reduces aggression from adults and, thus, facilitates flocking with adults. The cryptic hypothesis (Ewald and Rohwer 1980) argues that young birds are inconspicuous in winter to escape detection by predators or by dominant adult birds.

If a subdued first winter plumage is more valuable than a conspicuous first breeding plumage, and if spring molting is constrained, then subadult breeding plumages could be maladaptive. Both summer hypotheses presume subadult breeding plumages are adaptive, and both would be supported for any species in which prebreeding males grow femalelike feathers in spring. In contrast, if adult-

malelike feathers are grown in a spring molt, subadult plumages retained into the breeding season might more reasonably be viewed as a maladaptive constraint resulting from (1) some advantage of a subdued first winter plumage that overrides their breeding season cost, and (2) an inability to undergo a complete body molt in spring.

I initiated this study intending to distinguish between winter and summer explanations of the subadult plumage of Indigo Buntings (*Passerina cyanea*) by determining whether female-like feathers were regularly grown by subadult males in their first prealternate molt. I soon realized, however, that an unknown molt and subsequent plumage had to exist to explain the changed appearance of young males between fall and midwinter. Consequently, I describe the sequence of plumages and relate these discoveries to hypotheses of delayed plumage maturation.

METHODS

This study is based entirely on museum specimens, of which over 600 were examined from numerous collections (see Acknowledgments). The numbers of specimens upon which various conclusions are based are provided in the tables, figures, and text. Because the plumage descriptions provided by Dwight (1900) are adequate even for the previously unknown supplemental plumage, I supply only comparative notes on the various sex, age, and plumage classes.

I scored molt on percentage scales to facilitate future interspecific comparisons of the rate, intensity, and completeness of molts. All molt scoring was done under a LEDU (approximately $2\times$) magnifying lamp with a 60-W incandescent bulb for strong illumination.

Body molt was scored in five regions: (1) throat, the anterior undivided portion of the ventral tract; (2) breast, the middle portion of the ventral tract immediately anterior and posterior to its bifurcation; (3) belly, the posterolateral branches of the ventral tracts, including the flanks and belly feathers; (4) crown, the capital tract covering the crown of the head; and (5) back, the anterior and central region of the dorsal tract, excluding the rump. To check for the presence of underlying feathers that had been in active growth when the specimen was collected, body feathers were lifted with forceps at 3–8 points in each of the regions scored for molt. For each body region, I estimated the percentage of developing feathers using the following scale: 0 = no feathers in development, 10 = 1–20% of feathers in development, 30 = 21–40%, and so on to 90 = 81–100% of feathers in develop-

ment. Because body molts are sometimes very slow, I further divided category 10 as: 10A = 1 or 2 feathers in development, 10B = 3 or 4, 10C = 5 or 6, and 10+ = more than 6, but less than 20% of feathers in development. The percentage of body feathers in growth on a specimen was computed by averaging the molt scores for each of the five body regions, with the following conventions. To reduce error caused by feathers lost adventitiously, rather than by molting, I assigned molt scores of 0 to specimens showing less than 7 growing feathers in only a single body region and to specimens with small patches of incoming feathers that were all the same age and atypical of normal molt. Specimens with molt scores of 10A, 10B, or 10C in two or more body regions were considered to be in molt. In an effort not to overestimate the intensity of molt, I assigned total body molt scores of 10 to specimens having nonzero scores of 10A, 10B, or 10C in only two body regions.

Each remex and rectrix was scored on a scale of 0–1.0, by 0.1 intervals, to indicate the fraction of their full length that had been achieved. Empty follicles received a score of 0.1 because old feathers were given a score of 0. To qualify as molt rather than adventitious loss, a missing remex or rectrix had to be either the next feather in a sequence to be lost, or missing on both wings or both sides of the tail, thus marking the initiation of a molt sequence. Total primary molt scores were obtained by summing the scores for individual primaries.

For males the development of the alternate (breeding) plumage was measured quantitatively by summing the number of millimeters of spring blue feathers (solid, indigo-blue feathers) along four lines: (1) crown and nape, along the midline from the base of the upper mandible posteriorly 25 mm (includes all of the crown and part of the nape); (2) back, up the midline of the back from the level of the tips of the secondaries anteriorly 40 mm (excludes the nape); (3) throat and chest, along the midline from the base of the lower mandible posteriorly 30 mm (designed, on average, to reach the end of the breast feathers arising from the area of bifurcation of the ventral tract); and (4) flank, from the distal ends of the posterior-most flank feathers (those covering the specimen's ankle) 40 mm anteriorly along a line passing through the middle of the flank feathers and lying approximately parallel to the specimen's midline. Because adult males in breeding plumage are usually entirely indigo blue, the sum of blue measured along these lines divided by 135 mm (their total) estimates the percentage of body feathering in the definitive breeding color. After using this technique on winter-taken specimens, I became proficient at visually estimating these percentages; therefore, the percentages for spring-taken subadults from the United States were estimated.

For first-year males in any of the postjuvenile plumages, the color of developing feathers was re-

corded if the vane had emerged sufficiently from the sheath to reveal its color. This effectively categorized feathers either as part of the supplemental plumage (described herein) or as part of the first alternate plumage.

DESCRIPTION OF MOLTS

First prebasic molt.—Few specimens exist in full juvenile plumage because the first prebasic molt commences before the juvenile rectrices are fully grown, probably while the young are still being fed by their parents. This molt occurs while birds are on the breeding grounds; specimens showing active molt occur from early July until late October, and some early-fledged individuals must molt in June as 2 juveniles collected in July were already in their first basic plumage (Table 1). The peak intensity of this molt occurs in specimens nearing completion of the growth of their juvenile rectrices. The 5 specimens examined at this stage (all with nearly full-length rectrices that were still ensheathed at their bases) had an average 78% of their body feathers in growth; 2 of these 5 specimens had more than 80% of their feathers growing in all body regions.

Presupplemental molt.—This molt is confined exclusively to first-year birds and has not been recognized previously (e.g. Dwight 1900, Johnston and Downer 1968, Taber and Johnston 1968). It includes the outer primaries (typically starting at P3, 4, or 5) but not their coverts, the innermost secondaries (S7-9, rarely S6) and the secondary coverts, all rectrices, and, typically, all of the body plumage. I examined specimens from almost all U.S. collections with significant material from Mexico and Central America, and found only 15 specimens in this presupplemental molt showing both primaries and body feathers in development; 9 additional specimens, most at the terminal stages of this molt, showed only body molt (Figs. 1 and 2, Table 2). The molt itself is very intense, apparently reaching a peak about the time primary 9 is dropped; the only two specimens at this stage had 86% and 90% of their body feathers in molt. Thus, when the presupplemental molt is at peak intensity individuals presumably would have more than 80% of their body feathers, all of their rectrices, the outer 3 or 4 primaries, and secondaries 7 and 9 growing simultaneously.

Which primary initiates this molt varies considerably among individuals. Because almost no

TABLE 1. Date, plumage, and molt categories for birds of the year (males only) taken on the breeding grounds.*

	Juvenile plumage (not molting)	Active first prebasic molt	First basic plumage (not molting)	Active pre-supplemental molt	Supplemental plumage (not molting)
1-15 June	1	0	0	0	0
16-30 June	1	0	0	0	0
1-15 July	0	1	1	0	0
16-31 July	1	4	1	0	0
1-15 Aug	0	5	3	0	0
16-31 Aug	1	4	3	1	0
1-15 Sept	0	6	3	0	0
16-31 Sept	0	3	5	1	0
1-15 Oct	0	3	5	2	0
16-31 Oct	0	2	2	0	0
Total	4	28	23	4	0

* Samples only from specimens at the USNM, Field, and UW (see Acknowledgments).

individuals replace primaries in the prealternate molt, the number of primaries replaced in this presupplemental molt can be assessed easily in subadult males and females collected in summer on the breeding grounds. Most specimens initiated this molt with primary 4 or 5 (row totals of Table 3). This made it possible to measure the difference in length between P4 and P5 in specimens that had molted either P4 and P5 in the presupplemental molt or P5 but not P4 in the presupplemental molt. The difference between these means shows that the primaries grown in the presupplemental molt are longer than the juvenile primaries. Individuals with P4 old (and P5 new) had a mean distance between the tips of P5 and P4 of 4.64 mm (SD = 0.811, $n = 35$); those with P4 and P5 new had a mean distance of 3.77 mm (SD = 0.452, $n = 30$). I eliminated specimens in which either P4 or P5 was sufficiently worn to affect this measurement. The difference between these means suggests the fourth primary is 0.7 mm longer in the supplemental than in the juvenile plumage ($P < 0.001$); presumably, the outermost primaries, which are about $1.2\times$ longer than P4, would be proportionately longer.

The rate and duration of primary growth were estimated for birds undergoing the presupplemental molt on the wintering grounds by summing the primary development scores, starting at P5 (Fig. 2). Birds that had not re-

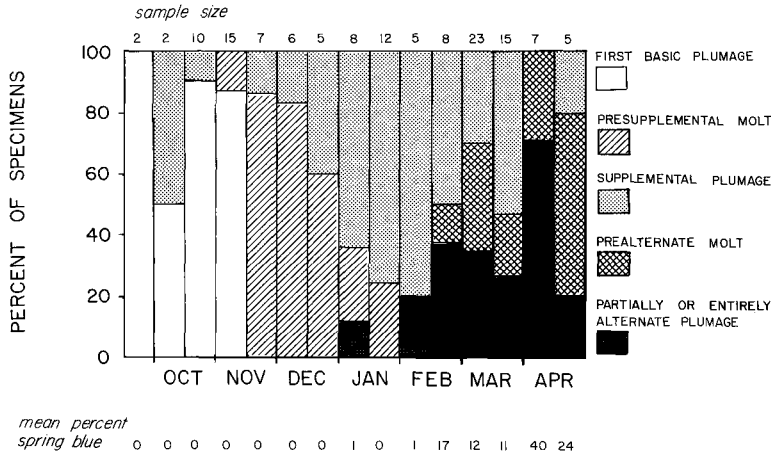


Fig. 1. Molts and plumages of male Indigo Buntings during their first winter. This figure is based exclusively on birds taken south of the United States.

placed P5 received a 1.0 for that feather, and birds that had replaced P3 or 4 received no points for those feathers. I started at P5 because this primary initiates the primary molt sequence more frequently than any other (row totals of Table 3). The maximum possible score was 5.0. The linear regression (Fig. 2) suggests that individuals require 23 days to replace completely primaries 5-9 (see Pimm 1976 for statistical methodology). Because most of the body molt is completed by the time the ninth primary is fully grown, the entire presupplemental molt takes slightly more than 3 weeks.

This presupplemental molt typically begins with the first primary lost, as indicated by two specimens each with a primary molt score of 0.2 and each with a mean body molt score of 0.67. Replacement of body feathers is well under way, and all of the secondary coverts and the rectrix coverts are simultaneously lost and fully replaced before S8 is lost. The rectrices are molted soon after the initiating primary is lost (and before the rectrix coverts are fully replaced) and are fully grown before P9 is fully replaced. For the 8 first-winter specimens exhibiting active rectrix molt, 3 had some outer rectrices that were very slightly behind some inner rectrices (the typical centrifugal sequence for passerines), 1 showed no sequence (no pin feathers were showing: UW 37733), and 4 had all rectrices of similar length (i.e. their tips were 4 mm different in length). S8 is lost and fully replaced, and then S7 and S9 are replaced simultaneously. This secondary replace-

ment occurs about midway through the primary replacement. S6 occasionally is replaced in this molt, but no specimen was growing this feather, so I do not know when it is replaced relative to the other secondaries. I could discern no sequence of progression in the body molt, perhaps because the molt is so nearly simultaneous. The primaries are lost sequentially, from inside to outside, and, frequently, three feathers are growing simultaneously in one wing.

The presupplemental molt usually occurs on

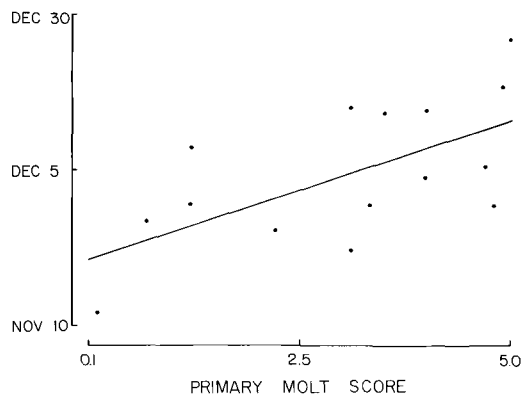


Fig. 2. Estimate of the duration of the presupplemental molt in first-year Indigo Buntings taken south of the United States. The primary molt scores of 0.1-5.0 usually bracket in time the feather replacement that takes place in other body regions. (See text for methodological information.)

TABLE 2. Date and numbers of yearling females collected on the wintering ground in various plumages and molts. This table may be compared with Fig. 1 for yearling males except that the spring and winter plumages cannot be distinguished for yearling females.

Date	First basic plumage (no body molt; juvenile P's)		Supplemental or first alternate plumage (outer P's new)		Total
	Pre-mental molt (body or P's)	Supplemental molt (body or P's)	Pre-mental molt (outer P's new)	First prealternate molt (outer P's new)	
1-15 Sept	2	0	0	0	2
16-30 Sept	0	0	0	0	0
1-15 Oct	0	0	0	0	0
16-31 Oct	12	0	0	0	12
1-15 Nov	7	1	1	0	9
16-30 Nov	1	1	1	0	3
1-15 Dec	0	1	3	0	4
16-31 Dec	0	0	5	0	5
1-15 Jan	0	0	5	0	5
16-31 Jan	0	0	4	0	4
1-15 Feb	0	0	1	0	1
16-29 Feb	0	0	2 ^a	0	2
1-15 Mar	0	0	4	3	7
16-31 Mar	0	0	3	2	5
1-15 Apr	0	0	4	4	8
16-30 Apr	0	0	0	3	3
Total	22	3	33	12	70

^a Includes LSU 20848 with molt arrested and only part of the outer primaries replaced.

the wintering grounds (Fig. 1) but occasionally occurs on the breeding ground (Tables 1 and 2). The frequency of first-year birds (males and females) that molt prior to fall migration was calculated from those specimens taken on the wintering grounds prior to 16 November. This cut-off date should be virtually without bias because there is no evidence that first-year birds

molt on the wintering grounds prior to early November, and birds that begin in early November (Fig. 1, Table 2) should not have finished replacing their primaries by 15 November (Fig. 2). Only 3 of 52 (6%) first-year birds (2 males, 1 female) had completed the presupplemental molt while on the breeding grounds. This frequency was more crudely estimated from specimens taken in the United States as $S/(B + S)$, where S is the number of specimens partially or entirely in the supplemental plumage and B is the number of specimens entirely in the first basic plumage. This method indicates 4 of 27 (15%) young males (females were not examined) were undergoing the presupplemental molt prior to fall migration, but the figure is surely an overestimate because many specimens still in the first prebasic molt are eliminated from the denominator (see Table 1). Of the 28 individuals so eliminated, most could not have had time to undertake the presupplemental molt before migrating; thus, I think it best to assume that less than 10% of hatchling birds undergo the presupplemental molt before migrating.

The conclusion that the supplemental plumage is confined exclusively to young birds is based on three points. First, only 16% of 25 adults taken between 16 November and 31 December were in molt (Table 4), whereas 100% of the first-year birds that had not undergone the presupplemental molt before migrating were molting in this same period. Second, the percentage of growing body feathers on birds taken in molt was high in young birds but not in adults between 16 November and 31 December (Table 5). Adults in active body molt in this period had 4-30% of their feathers in molt (mean = 12%); body molt scores for first-year birds were much higher, some individuals hav-

TABLE 3. Completeness of the prealternate molt and the number of primaries replaced in the presupplemental molt for young males.

Primaries replaced in presupplemental molt	Percent spring blue ^a											Total
	0	10	20	30	40	50	60	70	80	90	100	
1-, 2-, or 3-9	1	1	1	1	0	0	1	1	2	1	6	15
4-9	0	2	2	4	2	1	2	5	3	8	16	45
5-9	0	0	5	2	0	5	5	11	10	8	12	58
6-, 7-, or 8-9	0	1	0	1	0	1	1	0	4	1	2	11
Total	1	4	8	8	2	7	9	17	19	18	36	129

^a Percentage of body feathers replaced in the first prealternate molt.

TABLE 4. Date, molt frequencies, and plumage condition of adults taken on the wintering grounds.

Date	Adult females		Adult males			
	Percent in body molt	<i>n</i>	Percent in body molt	Percent with some new inner S's	Mean percent spring blue ^a	<i>n</i>
1-15 Sept	—	0	0	0	0	1
16-30 Sept	—	0	—	—	—	0
1-15 Oct	—	0	0	0	0	2
16-31 Oct	0	12	0	0	0	11
1-15 Nov	0	4	0	0	0	7
16-30 Nov	33	3	—	—	—	0
1-15 Dec	0	5	20	0	1	5
16-31 Dec	0	7	40	0	1	5
1-15 Jan	25	4	0	0	9	7
16-31 Jan	0	6	27	0	18	15
1-15 Feb	0	1	38	25	33	8
16-29 Feb	0	2	44	67	43	9
1-15 Mar	0	5	50	20	52	10
16-31 Mar	0	2	50	75	68	12
1-15 Apr	75	4	50	75	90	4
16-30 Apr	50	2	0	100	100	2
1-15 May	—	0	100	100	100	1
Total		57				99

^a Mean percentage of body feathers replaced in the first prealternate molt.

ing over 80% of their body feathers in growth (mean = 33%, Table 5). Third, adults replaced no primaries in winter (sample sizes in Table 4), whereas first-year birds did. One adult female (AMNH 707245) taken on 15 November in Mexico was finishing the primary and secondary molt. This bird must have been completing her prebasic molt when collected because most of secondaries 1-6 (which are never replaced in the presupplemental molt) show bits of sheathing at their bases.

Prealternate molt.—This protracted molt occurs in all sex and age classes (Table 5: mid-winter-spring), but is often less complete in young males than in adult males. As a result, the first breeding plumage is usually a mix of the indigo-blue alternate plumage and the much less conspicuous whitish or brownish supplemental plumage. For some first-year males I recorded the color of feathers of the first alternate plumage that had been growing when the specimen was collected. In 16 specimens taken in March, April, and May every feather that could be scored was indigo blue (the adult male breeding color); on one additional specimen (AMNH 398031), one crown feather and three auriculars were indigo blue, but two other growing auriculars were brown and femalelike. A number of other specimens (count not recorded) showed indigo-blue

feathers, but no others showed brown, femalelike incoming feathers.

In adult males the prealternate molt typically includes all body feathers, the secondary coverts, and 7-9 of the inner secondaries; the rectrices, the primaries, and the primary coverts are not replaced in adults. In young males in which the molt includes secondaries or their coverts, some or all of the greater secondary coverts are more likely to be replaced than are any of the inner secondaries. A very few specimens (number not recorded) had a fresh middle primary (e.g. P5 new in both wings of USNM 83754 and 338124), indicating that birds occasionally will replace a middle primary at the first prealternate molt. I found no evidence that this reinitiation of the primary molt ever leads to a second replacement of all the outer primaries in first-year birds.

Two questions may be raised with regard to females: first, is the prealternate molt less complete in first-year than in adult females, as is the case for males? Second, because neither adult nor first-year females change color, is this molt less complete in females than in males? Because females show no color change and only minimal amounts of feather wear, I was forced to address these questions by two indirect methods. First, comparisons of molt intensities for the various age and sex classes revealed no

obvious differences either between the female age classes or between males and females (Table 5), but samples of females were minimal. Second, there were no differences either for adults or for first-year birds in frequencies of specimens in active molt taken south of the United States from 1 March to 15 May, the period when the prealternate molt is most intense. For adults, 4 of 13 females and 15 of 29 males were molting (Table 4; $\chi^2 = 0.64$, $P \approx 0.40$), and for first-year birds 12 of 23 females and 16 of 50 males were molting (Fig. 1, Table 2; $\chi^2 = 1.15$, $P \approx 0.30$).

The completeness of the prealternate molt can be compared in males (because of their color change) with the number of primaries replaced in the presupplemental molt (Table 3). If the completeness of these molts depends on a bird's condition or food supply, then individuals in good condition or with greater access to food might be expected to replace more feathers than average in both of these molts and vice versa. When the data (Table 3) were analyzed with a standard median test (dividing the data between 70% and 80% spring blue), no significant association between the number of feathers replaced in these molts was obtained ($\chi^2 = 0.53$, 1-tailed $P \approx 0.25$). However, subadults that had replaced 90–100% of their body feathers in the prealternate molt also had replaced more than the median number of primaries in the supplemental molt (90–100%: $\chi^2 = 3.37$, 1-tailed $P \approx 0.03$; 100%: $\chi^2 = 4.28$, 1-tailed $P \approx 0.02$). Because there is so much variability in the extent of the prealternate molt, perhaps an effect of individual quality can be seen only by considering individuals that are well above median feather replacement in this molt.

Surprisingly, 17% of subadult males taken in the U.S. between 15 April and 31 May were in active prealternate molt when collected (Table 6). The intensity of this molt diminished between mid-April and the end of May (Table 6A). That some subadults molt during migration is confirmed by a specimen (USNM 564188) killed in migration the night of 5–6 May 1960 in Indiana when it struck a building. Ten percent of its body feathers were growing.

Individuals that had replaced less of the supplemental plumage while on the wintering grounds were much more likely to show active molt in early spring in the United States than were individuals that had replaced most of the supplemental plumage (Table 6B; $\chi^2 = 12.3$,

TABLE 5. Date and mean percentage of body feathers growing for birds taken on the wintering grounds while in active molt. The five body regions scored to estimate the percentage of feathers in molt were crown, back, throat, breast, and belly. Sample sizes are given in parentheses.

Date	Yearlings		Adults	
	Males	Females	Males	Females
1–15 Nov	6.0 (2)	2.0 (1)	— (0)	— (0)
16–30 Nov	37.3 (6)	26.0 (1)	— (0)	4.0 (1)
1–15 Dec	42.0 (5)	22.1 (1)	10.0 (1)	— (0)
16–31 Dec	18.0 (3)	— (0)	17.0 (2)	— (0)
1–15 Jan	9.0 (2)	— (0)	— (0)	12.0 (1)
16–31 Jan	2.0 (3)	— (0)	11.2 (4)	— (0)
1–15 Feb	— (0)	— (0)	24.2 (3)	— (0)
16–29 Feb	6.0 (1)	— (0)	12.0 (4)	— (0)
1–15 Mar	14.5 (8)	11.3 (3)	29.8 (5)	— (0)
16–31 Mar	13.6 (3)	26.0 (2)	31.9 (6)	— (0)
1–15 Apr	5.0 (2)	8.5 (4)	16.0 (2)	36.3 (3)
16–30 Apr	3.8 (3)	4.0 (3)	— (0)	12.0 (1)
1–15 May	— (0)	— (0)	6.0 (1)	— (0)

$P < 0.001$). While scarcely surprising, this result strongly suggests that spring feather replacement in the U.S. represents a continuation or a resumption of the prealternate molt, rather than adventitious feather loss, because adventitious pulling of feathers should affect old and new feathers alike. It also suggests that the dull subadult plumage is sufficiently disadvantageous in the breeding season that resources that might be invested more directly in the breeding effort are instead invested in acquiring a more completely adult-malelike body color.

PLUMAGE COMPARISONS

Birds in juvenile plumage can be distinguished by the very lax feather vanes of the juvenile plumage and by the narrow and distinct streaking on the breast and flank that contrasts with the vague striping shown by some adult females and by some birds in the first basic plumage. For individuals in which the first prebasic molt seems complete, the flank feathers should be checked as these feathers are often molted late and show the textural differences between juveniles and older birds particularly well. Birds in first basic plumage may be distinguished from females in the definitive basic and the definitive alternate plumages only by the appearance of their primary coverts. These are without blue and, in late summer and fall, more lax (being slightly "fuzzier," especially on the edge of their vanes) than those

TABLE 6. Prealternate molt during or after the spring migration; data are for subadult males taken in the United States.

(A) Number of individuals molting and the average of the mean body molt scores for specimens in active molt

Date	Sample total	Number molting	Percent molting	Mean body molt score (SD)
15-30 Apr	12	2	17	29.0 (9.90)
1-15 May	36	10	28	7.4 (4.99)
16-31 May	68	8	12	8.8 (8.81)
Total	116	20	17	—

(B) Percent spring blue^a vs. frequency of subadults in molt during April and May

Percent spring blue	Number molting	Number not molting	Percent molting
0-25	6	9	40
26-50	5	15	25
51-75	6	20	23
76-100	3	52	5
Total	20	96	17

^a Percentage of body feathers replaced in the first prealternate molt.

of adults. This difference is difficult to assess without experience and requires good light and a hand lens or other source of low magnification. The method, however, is infallible with proper experience.

I found no feature of the body plumage that distinguishes the sexes either in the juvenile plumage (very small samples) or in the first basic plumage (more than 48 males and 22 females compared). Dwight (1900), however, reported that rectrices of juvenile males have a bluish or greenish tint while those of juvenile females are browner. Because the juvenile rectrices are not replaced in the prebasic molt, this color difference could distinguish the sex of all young birds in fall and early winter. Unfortunately, I did not adequately assess its reliability, but 5 females and 3 males in the UW collection did not overlap in rectrix color. Thus, it may be possible to sex young birds both in juvenile plumage and in first basic body plumage from the presence (for males) or absence (for females) of a bluish tint on the rectrices.

Obvious sexual difference is first achieved in the supplemental plumage. In this plumage young males become distinguishable from

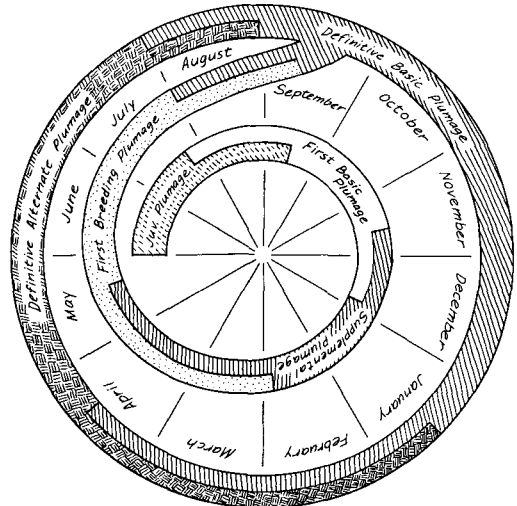


Fig. 3. Summary of the development of the body plumages in Indigo Buntings. Symbols identify feather coats that look different in males, and periods of overlap between plumages symbolize periods of molt. The "first breeding plumage" is often a mix of supplemental and first alternate feathers. Females have the same molts and plumages but without color changes. The polymorphic timing of the presupplemental molt is not illustrated.

young and adult females by the assumption of a scaly blue appearance, particularly on their breasts and bellies. This is caused by the body feathers having bluish centers, even though these feathers are sometimes so broadly tipped with brown (or white on the belly) that overlying feathers on occasional specimens in very fresh plumage must be lifted for the blue to be apparent. Because up to 10% of young undergo the presupplemental molt before fall migration, it is essential, *even in fall and early winter*, that the primaries or primary coverts of males in the scaly blue adult plumage be examined for an accurate determination of their age by plumage characters.

From midwinter until the end of the following summer, young birds of both sexes are easier to distinguish from adults by the break in the appearance of their primaries than by the condition of their primary coverts. In young birds the innermost primaries (usually 1-3 or 4), which are not replaced in the presupplemental molt, are more faded and worn than the outer primaries. In adults all of the primaries form a continuous series in appearance. The presence or absence of a break in the primary

series is easy to evaluate in both sexes, and the condition persists until the end of the first potential breeding season because primaries are almost never replaced in the prealternate molt. Condition and color of the primary coverts also will distinguish accurately yearling and adult females (as well as males) in the breeding season, but these characteristics are more difficult to assess on females than is the presence or absence of a break in the primary sequence.

The comparative appearance of the fall and winter plumages of Indigo Buntings may be summarized as follows. The three postjuvenile plumages worn by yearling females (Fig. 3) are indistinguishable grossly and resemble the definitive plumages of older females. These plumages differ in yearling males, in which the first basic resembles the definitive basic of adult females, the supplemental resembles the definitive basic of adult males, and the first alternate resembles the definitive alternate of adult males (Fig. 3). Although the feathers acquired by young males in the first prealternate molt mimic those of the definitive alternate breeding plumage, there is considerable variability among first-spring males because individuals differ in how much of the supplemental plumage they replace.

Neither the presupplemental molt of young males nor the prealternate molt of young and old females appears to be required to replace worn feathers. Indeed, feather wear is highly implausible as an explanation of the presupplemental molt in either sex because the preceding basic plumage is worn for less than 3 months in most birds. I believe the reason females undergo the presupplemental and prealternate molts is that these molts occur in males to produce color changes, and the genes that produce these molts in males also produce them in females, despite their probable cost to females. Lande (1980) showed that high genetic correlations between homologous characters of males and females cause the attainment of sexual dimorphism to be very slow. Thus, characters that originate because of benefits limited to only one sex may persist in the other sex for many generations (Lande 1980).

IMPLICATIONS TO THEORIES OF DELAYED PLUMAGE MATURATION

Summer explanations of delayed plumage maturation invoke various aspects of social

competition and communication in the first potential breeding season as causes for subadult breeding plumages. In contrast, winter explanations invoke social competition and communication in the first winter as the causes for delayed plumage maturation and do not necessarily ascribe an adaptive function to the subadult breeding plumage. Comparative data for more than 100 North American passerines in which adults are sexually dichromatic either in winter or in summer suggest that in winter the subdued plumages of first-year males are adaptive. The following shared patterns support this view. First, every species that features a subdued first breeding plumage in males also features a femalelike first winter plumage in males. Second, in many species young males change in spring to be less like adult females and more like adult males than they were in fall. Finally, in no species are young males more like adult males in winter than they are in spring (Rohwer and Butcher unpubl.).

The previously unknown supplemental plumage of first-year Indigo Buntings strongly supports a winter explanation of delayed maturation for this species. The completeness of the presupplemental molt implies that the femalelike first basic plumage shed by young males in this molt can only be a response to conditions of the first fall or the beginning of the first winter. Furthermore, the supplemental plumage of young males exactly "mimics" the winter plumage of adult males, which is dramatically different from and independent of the adult-male breeding plumage because the prealternate molt of adult males includes virtually all body feathers in most individuals. Although the first prealternate molt of young males is often incomplete, the supplemental plumage of young males still must be related to social competition during winter because this plumage is exactly like the definitive basic plumage of wintering adult males, which, in turn, is known to be independent of summer demands. Presumably, the supplemental plumage facilitates a midwinter change in the social relationships between young males and other Indigo Buntings, but why supplemental plumages are unreported for other passerines remains unresolved.

The feathers grown by young males in the first prealternate molt are virtually always the color of the definitive alternate breeding plumage of adult males. This fact argues against a

summer explanation of the subadult breeding plumage of young males. If a subdued first breeding plumage were advantageous, female-like feathers should regularly be produced in this molt.

Energetic costs of the prealternate molt do not seem to have been studied for any species (Payne 1972, King 1980, Walsberg 1983). Even though the prealternate molt includes only body feathers in most species, it seems very likely to impose significant foraging costs. Three recent reviews of the cost of molting provide data on temperate-region passerine species; most show a 10–40% increase in basal metabolic rate for the duration of the prebasic molt (Payne 1972, King 1980, Walsberg 1983). In these species, the energetic demands of molt are met by delaying the molt until after breeding, by a general decrease in activity by molting birds, and by compensatory increases in foraging (Payne 1972, King 1980, Walsberg 1983). Prealternate molts, occurring at the end of winter, contrast critically with prebasic molts because their energetic demand cannot be met by reducing other activities. The primary activity of wintering birds is feeding themselves; thus, the energetic demands of the prealternate molt must be met primarily by an increase in food intake. At the end of winter this may be difficult or impossible for yearlings of some species to achieve. This food-limitation hypothesis merits testing by evaluating whether *ad libitum* feeding results in a more complete prealternate molt by yearling males in species that feature variability among subadults in the extent of the prealternate molt.

The hypothesis that dull first breeding plumages are a maladaptive consequence of late-winter food shortages is consistent with the prealternate molt being resumed or continued in the United States by subadult males in which it was substantially incomplete prior to the spring migration (Table 6B). The benefit of using resources for further advancing this molt rather than for activities more directly associated with breeding is perhaps explained by Payne's (1982) finding that young males with more indigo-blue feathers in their first summer are more successful at breeding. Completing more of the prealternate molt after migrating may assist a subadult male to obtain a female later in his first breeding season.

The timing of the prealternate molt of adults relative to the presupplemental molt of sub-

adults has the appearance of an arms race (Dawkins and Krebs 1979) between young and old males and between individuals within these age classes. Such a metaphor seems reasonable if the presupplemental molt of young males, which changes their appearance from brown to a mottled blue similar to winter adult males, evolved as a status signal (see Rohwer 1975, 1982). To elaborate, most young males arrive on the wintering ground looking like females. Yet, within one or two months of their arrival, they exchange this femalelike plumage for one that "mimics" that of adult males almost perfectly. Under status-signaling assumptions, young males should change color after they have gained enough experience to dominate adult males or females and are able to benefit from a signal indicating that ability. Coincident with this molt by young males, some adult males begin to replace their winter body feathers with summer feathers that are solid indigo blue (Tables 4 and 5). Some subadult males also initiate their first prealternate molt very early in winter, within weeks of the time that the supplemental plumage is normally acquired (Fig. 1). Perhaps those males that initiate the prealternate molt so early are socially high ranked and benefit from patches of indigo-blue feathering that advertise their high status.

Why is it that only about 10% of first-year males undergo the presupplemental molt while on the breeding grounds? Only the earliest fledged young may have time to molt prior to the fall migration, but time seems ample for more than 10% to do so because Indigo Buntings are late migrants (Table 1; Johnston and Downer 1958). If, as I argue, time is not a constraint, the variable timing of this molt relative to the fall migration may represent a frequency-dependent equilibrium. Such an equilibrium could be maintained either because the costs of mimicking adult males or because the benefits of a femalelike plumage accrue in a frequency-dependent fashion. A frequency-dependent cost of conspicuousness seems more likely simply because the colorfulness of the supplemental plumage must signal something. I expect that the colorfulness of this plumage will prove to elicit aggression from adult males. Whatever the specific cost, the essential feature for a frequency-dependent argument is that the cost per individual of the supplemental plumage increases with the frequency of young males that acquire it before the fall migration.

Given this, it is theoretically possible—at some (equilibrium) frequency—for the net benefits of mimicking adult males in early winter to be equal to the net benefits of carrying a female-like plumage in early winter. The femalelike first basic plumage may benefit young males either by rendering them inconspicuous to predators or adults (Ewald and Rohwer 1980) or by reliably signaling their subordination to and, thus, facilitating their association with adults (Rohwer and Ewald 1981).

That the supplemental plumage of young males resembles the plumage of winter adult males (rather than of summer females) deals a crippling blow to the female mimicry hypothesis for Indigo Buntings and perhaps other species as well (Rohwer et al. 1980, Rohwer 1983, Flood 1984). Because the first prealternate molt is often incomplete, many young males retain a portion of the supplemental plumage for the breeding season. This subadult breeding plumage more resembles the brownish appearance of breeding females than the indigo blue of breeding adult males. It is, nonetheless, incorrect to speak of female mimicry when the feathers in question actually resemble those of *adult males* in winter plumage.

ACKNOWLEDGMENTS

I have benefited from discussing this work with Dolph Schleuter, Greg Butcher, Mart Gross, and Nancy Flood, and I thank Ken Parkes, Greg Butcher, Nancy Flood, Ken Yasukawa, and Cristine Soliz for help on various drafts of the manuscript. Arn Slettebak kindly constructed Fig. 3. Curators at the following institutions lent specimens or provided access to their collections: American Museum of Natural History (AMNH), Field Museum (Field), U.S. National Museum (USNM), Moore Laboratory of Zoology at Occidental College, Louisiana State University (LSU), Harvard University, University of Minnesota, University of Michigan, Delaware Museum of Natural History, University of Washington (UW), University of California at Los Angeles, Yale University, Royal Ontario Museum, Carnegie Museum of Natural History, University of California at Berkeley, Los Angeles County Museum, and California Academy of Sciences. I am especially grateful to Wesley Lanyon at the American Museum, who assumed responsibility for loans sent to me, and to Mary LeCroy and Ivy Kuspit for their helpfulness while I worked at the American Museum. This work was partly supported by a grant from the Harry Frank Guggenheim Foundation and by NSF grant BNS 80-08957.

LITERATURE CITED

- DAWKINS, R., & J. R. KREBS. 1979. Arms races between and within species. *Proc. Royal Soc. London, Series B* 205: 489-511.
- DWIGHT, J., JR. 1900. The sequence of plumages and moults of the passerine birds of New York. *Ann. New York Acad. Sci.* 13: 73-360.
- EWALD, P. W., & S. ROHWER. 1980. Age, coloration and dominance in nonbreeding hummingbirds: a test of the asymmetry hypothesis. *Behav. Ecol. Sociobiol.* 7: 273-279.
- FLOOD, N. J. 1984. Adaptive significance of delayed plumage maturation in male Northern Orioles. *Evolution* 38: 267-279.
- JOHNSTON, D. W., & A. C. DOWNER. 1968. Migratory features of the Indigo Bunting in Jamaica and Florida. *Bird-Banding* 34: 277-293.
- KETTERSON, E. D. 1979. Status signaling in Dark-eyed Juncos. *Auk* 96: 94-99.
- KING, J. R. 1980. Energetics of avian molt. *Proc. 17th Intern. Ornithol. Congr.*: 312-317.
- LACK, D. 1954. *The natural regulation of animal numbers.* Oxford, Clarendon Press.
- LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34: 292-305.
- PAYNE, R. B. 1972. Mechanisms and control of molt. Pp. 103-155 *in Avian biology*, vol. 2 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- . 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in Indigo Buntings. *Ecology* 63: 401-411.
- PIMM, S. 1976. Estimation of the duration of bird molt. *Condor* 78: 550.
- ROHWER, S. 1975. The social significance of avian winter plumage variability. *Evolution* 29: 593-610.
- . 1982. The evolution of reliable and unreliable badges of fighting ability. *Amer. Zool.* 22: 531-546.
- . 1983. Testing the female mimicry hypothesis of delayed plumage maturation: a comment on Procter-Gray and Holmes. *Evolution* 37: 421-423.
- , & P. W. EWALD. 1981. The cost of dominance and advantage of subordination in a badge signaling system. *Evolution* 35: 441-454.
- , S. D. FRETWELL, & D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Amer. Natur.* 115: 400-437.
- , W. P. KLEIN, JR., & S. HEARD. 1983. Delayed plumage maturation and the presumed prealternate molt in American Redstarts. *Wilson Bull.* 95: 199-208.
- SILANDER, R. K. 1965. On mating systems and sexual selection. *Amer. Natur.* 99: 129-141.

TABER, W., & D. W. JOHNSTON. 1968. *Passerina cyanea* (Linnaeus), Indigo Bunting. Pp. 80-111 in *Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies* (O. L. Austin, Jr., Ed.). U.S. Natl. Mus. Bull. 237, part 1.

WALSBERG, G. E. 1983. Avian ecological energetics. Pp. 161-220 in *Avian biology*, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

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The prepublication review process is essential to the maintenance of high scientific standards in a journal. The efforts of the individuals who contributed reviews, both singly and together, are remarkable. Each has been thanked personally, but deserves this public acknowledgment. The memorials for volume 102 were solicited and managed by C. Stuart Houston.

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