

## ANNUAL MOLTS AND INTERRUPTION OF THE FALL MIGRATION FOR MOLTING IN LAZULI BUNTINGS<sup>1</sup>

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**Abstract.** Lazuli Buntings, *Passerina amoena*, interrupt their fall migration in the American Southwest to undergo the major portion of their fall molt. Adults molt only limited numbers of body feathers on the breeding grounds before migrating to one of two molting "hotspots," (1) a region bounded by southern Arizona, southwestern New Mexico, and northern Sonora or (2) southern Baja California. Here they molt the rest of their body feathers and all flight feathers, before continuing on to the winter range in western Mexico. Hatching-year birds undergo a limited prebasic molt on the breeding grounds and then stop during migration at one of the same two hotspots to undergo a nearly complete presupplemental molt of all body and most flight feathers. Some individuals of both age classes also migrate directly to western Mexico to molt on the wintering grounds. A possible cause of the interrupted migration strategy is the combination of dry, food-scarce conditions on the breeding range and locally rainy, food-rich conditions at the molting stopovers from late August through October.

After the presupplemental molt, males and females are similar in color to adults in definitive basic plumage. The prealternate molt is limited to a few head feathers for all age/sex classes, with most color change from winter to breeding aspect resulting from wear of buff feather tips which obscure bright male colors during the winter. The definitive prebasic molt takes place August to October, involving replacement of all feathers. This molt is different in timing, location, and extent from that recently reported for two congeners, the Indigo Bunting, *P. cyanea*, and the Painted Bunting, *P. ciris*.

**Key words:** *Interrupted migration; Lazuli Bunting; Mexico; molt; molt-migration; museum specimens; Passerina amoena.*

### INTRODUCTION

Birds molt both to replace worn feathers and to change their appearances in either social signaling or predator avoidance contexts. Molt is costly, however, as several studies have shown that birds raise their basal metabolism by 9–46% while in molt (Lustick 1970, Gavrilov 1974, Chilgren 1975). Intense molt is thus on a par with reproduction and migration as a major energetic demand in the annual cycle (Payne 1972, Walsberg 1983). Yet despite its importance, molt is much less studied than reproduction and migration. For North America, few species have been studied in depth, so most of our knowledge of molts comes from older general summaries lacking in quantitative data (e.g., Dwight 1900, Forbush 1924, Dickey and Van Rossem 1938). Especially lacking are studies of western North American birds (Rohwer and Manning 1990) where pre-

viously unknown and unexpected patterns are turning up. For example, Willoughby (1986) discovered two complete molts in hatching year Cassin's Sparrow (*Aimophila cassinii*), and Rohwer and Manning (1990) documented that Bullock's Orioles (*Icterus galbula bullockii*) have very different molt and migration schedules from their eastern counterpart, the Baltimore Oriole (*Icterus galbula galbula*).

Here I document the sequence, extent, and timing of molts in the Lazuli Bunting, *Passerina amoena*, a migratory, sexually dichromatic passerine of western North America. No quantitative study of molt in this species has ever been undertaken; our knowledge is restricted to a few comments in Pyle et al. (1987) who largely assume the molt is identical to that of the Indigo Bunting. My goals for this study were: (1) to describe the annual molts; (2) to identify characters that can be used to determine age and sex classes of Lazuli Buntings; (3) to learn where the fall molt occurs and to speculate on what factors may have led to this pattern; and (4) to compare the

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molt cycle in Lazuli Buntings with the recently described molts of congeneric Indigo Buntings, *P. cyanea* (Rohwer 1986), and Painted Buntings, *P. ciris* (Thompson 1991). I present evidence that some, possibly most, Lazuli Buntings interrupt their fall southward migration to undergo a rapid molt, and I show that molt patterns vary markedly among these three congeneric buntings.

## METHODS

I based this study exclusively on information gathered from 665 museum specimens. I requested loans of Lazuli Bunting specimens from (1) every North American museum with holdings of over 10,000 specimens, and (2) smaller museums that are located within the range of the species (Banks et al. 1973; see Acknowledgments for sources of specimens and museum abbreviations). Since Nearctic passerines generally do not molt while breeding, I requested specimens that were collected in all months except May and June, the usual breeding season for Lazuli Buntings (Jewett et al. 1953, Erickson 1968). However, I examined 17 adult male specimens collected in May and housed at the AMNH for buff feather tip wear (see below). I use the molt terminology proposed by Humphrey and Parkes (1959) and the age class terminology used by the Bird Banding Laboratory and modified by Pyle et al. (1987). Age class terms used are hatching year (HY), birds that are in their first calendar year and that are in or have completed either their first prebasic or supplemental molt; second year (SY), birds in their second calendar year but before the second prebasic molt is so far completed that these are indistinguishable from older birds; after second year (ASY), birds collected after their second prebasic molt; and after hatching year (AHY), all SY and ASY birds.

*Scoring molt.* To avoid subjective bias, I covered each specimen label with a piece of paper on which the specimen number was written several weeks before examination. After scoring, I removed the covers and recorded the date, locality, and sex from the labels. In general, I followed the methods described by Rohwer (1986) for scoring molt which I briefly outline here, noting departures from this scheme where they occur.

I examined all specimens using a 2× magnifying lamp lighted with a 60-W incandescent bulb. I scored body molt in six regions: throat, breast, belly, crown, back, and rump (see Rohwer 1986

for definitions). In each region, I looked for growing feathers (i.e., feathers in sheaths) by lifting feathers with watch-makers forceps at 5–7 points. I estimated the percentage of feathers growing in each region using Rohwer's (1986) scale of 0, 10, 30, 50, 70, and 90% of feathers in development. In addition, I scored a body region as being in 100% molt if all feathers were in sheaths. If none or just one feather was in development, I scored the region as 0%; if two or more (up to 20% of the total) were in development, I scored the region as 10% molt. I then calculated a body molt score for each specimen as an average of the scores for the six regions. In addition, I scored feather wear for each body region and for the individual flight feathers on a 1–5 scale: 1 = fresh, 5 = extremely worn. I also noted the presence of feathers in more than one wear class, indicating they had been grown during different molt episodes.

For flight feather molt, I scored each primary on a 0–1.0 scale. Old feathers received a 0 score, and growing feathers received positive scores based on their lengths: empty follicles received 0.1; full grown feathers received 1.0; and partly grown feathers received from 0.2 to 0.9 depending on the fractional growth attained at the time of collection. The primary molt score was the sum of these individual feather scores. For computing the primary molt scores of specimens in the presupplemental molt, I summed scores distal to and including the fourth primary (P4), the remex at which this molt most commonly initiated. I recorded P4 as replaced in those few specimens where the molt was initiated at P5. Thus HY specimens could have primary scores from zero to six, and adults, which replace all primaries in the fall, from zero to nine. To determine the length of time over which flight feathers grow, I followed the regression method of Pimm (1976).

Early in the study it became apparent that male Lazuli Buntings change from their overall buffy winter aspect to bright summer blue, cinnamon, and white summer aspect primarily through feather tip wear, rather than through an extensive prealternate molt. To document this change in males, I scored the percent of feathers with any of their buffy tips remaining in the three dorsal regions plus the throat region. I averaged these four scores to obtain a "percent buff tip" score for each specimen. I did not score the breast region since the buff tip color blended in with

TABLE 1. Frequency of HY specimens from the breeding grounds molting from natal down into juvenal plumage (N → J), in juvenal plumage (J), in the first prebasic molt (J → B), and having completed the first prebasic molt (1B) in relation to date. As the first prebasic molt involves varying numbers of body feathers, a specimen having replaced any of its body feathers in this molt is defined as having completed the first basic molt.

	N → J	J	J → B	1B
16–30 June	5	0	2	0
1–15 July	2	1	6	1
16–31 July	7	2	13	10
1–15 August	6	2	20	8
16–31 August	2	3	10	26
1–15 September	1	6	5	17
16–30 September	0	2	1	9
1–15 October	0	1	0	1
Total	23	17	57	72

the underlying cinnamon. The white belly feathers did not consistently have buff tips after the fall molt, so I did not score these either. Tips of body feathers also wear in females, but again these blend well with the overall brown colored feathers making scoring unreliable. Since the buff tips were not completely gone in all late April specimens, I examined 17 additional adult males taken in May to form a complete picture of the loss of these tips. I then plotted the percent buff tip score for each specimen with its date of collection to examine the timing and rate of change from winter (buffy) to summer (bright blue, cinnamon, and white) aspect.

*Species, age, and sex identification.* Several specimens arrived misidentified as Lazuli Buntings (e.g., Young 1989). These were detected using the color and primary length characters described by Pyle et al. (1987).

I could determine the appearance of juvenal feathers by examining juveniles with all flight feathers in sheaths (i.e., individuals having recently fledged). Juvenal body feathers are of lower quality than the feathers which replace them in the limited first prebasic molt: they have a lower density of vanes along the rachis (see Rohwer and Manning 1990; Table 1) and adjacent vanes are more loosely attached to each other by the distal barbule hooklets (see Dwight 1900, Plate IV). Thus I could distinguish juvenal feathers from those grown in the first prebasic molt.

Second year Lazuli Buntings exhibit the pattern common to emberizid passerines in retain-

ing juvenal primary coverts (Dwight 1900). The all-brown juvenal coverts are easily distinguishable from the blue-edged brown ASY female and blue-edged dark ASY male coverts.

There is presently no known external character that can distinguish sexes of HY Lazuli Buntings either on the breeding grounds or in migration (Pyle et al. 1987). Rohwer (1986) suggested that rectrix color (flat brown versus brown with a blue sheen) may be a reliable character for the Indigo Bunting. In examining HY specimens, I discovered that wing bars are either whitish or buffy in color. Consequently I scored these two characters in HY specimens to determine if either could be used as a reliable sex character.

*Location and timing of molts.* To understand where and when molt events take place in the fall, I divided the breeding and winter ranges into segments encompassing 5° of latitude. I compared monthly profiles of the relative abundances of specimens taken from these segments in relation to the occurrence of molt to see where Lazuli Buntings most frequently molt. I combined this analysis with the use of mapped specimen locations to identify geographic "hotspots" of molting activity.

*Definition of winter and breeding ranges.* I defined the breeding range as that described in the AOU Checklist (American Ornithologists' Union 1983, p. 674–675): "southern British Columbia, southern Alberta, southern Saskatchewan, central North Dakota and northeastern South Dakota south to northwestern Baja California, southern California, southern Nevada, central Arizona, central New Mexico and central Texas, . . . and east to east-central Nebraska, western Kansas and western Oklahoma." The winter range is "southern Arizona and Chihuahua south to Guerrero and central Veracruz" (American Ornithologists' Union 1983:675). The 1983 AOU Checklist erroneously includes southern Baja California in the winter range. Wilbur (1987:150) lists the Lazuli Bunting as a "fairly common spring and fall migrant the length of the peninsula," but states that "there are no recent winter records for Baja California." I therefore consider southern Baja California as out of the normal winter range, but as a region where some wintering individuals may occur from time to time. Likewise, southern Arizona harbors very few wintering Lazuli Buntings (Root 1988).

*Statistical assumptions.* Series of specimens collected by myriad collectors over more than

100 years usually can not be expected to represent a random or systematic population sample that obeys assumptions of statistical tests. For instance, do four subadult male buntings collected on the same day from the same locality represent one observation or four? Surely they may share characteristics unique to their local gene pool or environmental conditions and would unfairly influence the overall sample if counted individually. On the other hand, if one specimen is in heavy molt and the rest are not, a simple average of the molt scores would distort any picture of the intensity of molt in the species. Therefore, to avoid flirting with pseudoreplication (*sensu* Hurlburt 1984), I shied away from using inferential statistics and relied instead on graphical and tabular analyses. I conducted standard statistical tests (Sokal and Rohlf 1981) where chances of violating assumptions about independence of data were minimal (i.e., analyses of a single age or sex class at a restricted time of year and geographical location with not more than one or two specimens per locality per year).

In addition, collecting effort is often biased by sex or age class, time of year, plumage, molt stage, or location (e.g., molting specimens may be underrepresented because they are hard to prepare and difficult to collect because of shyness). I assumed that these biases were consistent among all collectors. I also assumed that loss of sheathed feathers during specimen preparation or subsequent handling was inconsequential to my results. Finally, I assumed that no evolution of molt strategy occurred during the time that the specimens were collected.

## RESULTS

### DESCRIPTION OF MOLTS

*First prebasic molt.* HY Lazuli Buntings leave the nest in full juvenal plumage. Examination of "bob-tailed" specimens showed that all body feathers were of juvenal quality except for a few feathers on the lower back which were indistinguishable from adult quality feathers. In the 16 specimens with sheathed juvenal feathers, these back feathers are growing concurrently with the rest. Thus the adult-quality back feathers are unlikely to represent the beginning of a first prebasic molt.

The first prebasic molt occurs on the breeding grounds and can begin almost immediately after the juvenal feathers are fully grown. Only one of

the 58 specimens in this molt (USNM 130489 from the Arizona/Mexico border) was found south of the breeding range. Evidence for early onset comes from two molting specimens (SD 26875 and SD 26876) collected in late June. The percentage of specimens taken in this molt reaches a peak by early August and then declines through September (Table 1). This is a leisurely molt; the average of the body molt scores of specimens taken in the first prebasic molt was 3.9 ( $n = 56$ ), or about four percent of all body feathers growing.

In this molt, some but not all juvenal body feathers are replaced by adult-quality basic feathers. The most obvious color change occurs in the breast where streaky, off-white feathers are replaced by buff feathers. Off-white juvenal throat and belly feathers are replaced by first basic feathers of the same color, giving birds a distinct buff breast bar by late summer. Dorsally, brown juvenal feathers are replaced by darker brown first basic feathers. Several September specimens in full juvenal plumage were collected south of the breeding range in southern Arizona, southern New Mexico, and northern Sonora (e.g., UCLA 29302, USNM 235572, UNM 5199, MNA 2890). Since specimens in prebasic molt from these regions are so rare, it is likely that some individuals may molt directly from juvenal to supplemental plumage. The molt begins on the breast and back and then progresses to the crown, throat, and belly. The rump feathers are rarely replaced, and few individuals replace all juvenal feathers in any one region.

*Presupplemental molt.* At either a migratory stopover or on the wintering grounds, HY birds have another molt that includes all body feathers, all rectrices, the outer 4–7 primaries, and the inner 3–6 secondaries. The only feathers not replaced are the inner primaries, the outer secondaries, and some to all of the primary coverts. Color change in Lazuli Buntings is from brown juvenal to buff-tipped adult colors in both males and females. I call this a presupplemental molt for two reasons. First, this molt is in addition to the presumably ancestral fall prebasic and spring prealternate molts (following Humphrey and Parkes 1959). The prebasic molt begins and ends on the breeding grounds and leaves HY birds with a mix of juvenal and prebasic feathers distinguishable by quality in all body regions except the lower back and by color in the breast. Then the body feathers are replaced for the second time

TABLE 2. Extent of presupplemental wing molt based on feather wear differences in specimens collected after completing the presupplemental molt but before beginning the second prebasic molt. Sexes are summed as there was no difference in extent of molt between males and females (Kolmogorov-Smirnov two-sample test, primaries:  $D = 0.097$ , NS; secondaries:  $D = 0.109$ , NS; Sokal and Rohlf 1981).

Primaries replaced	Number of specimens showing pattern	Secondaries replaced	Number of specimens showing pattern
P1-9	0	S1-9	0
P2-9	4	S2-9	1
P3-9	35	S3-9	1
P4-9	73	S4-9	4
P5-9	28	S5-9	21
P6-9	0	S6-9	49
P7-9	0	S7-9	55
P8-9	0	S8-9	1
P9	0	S9	0

(or for the first time in the case of juvenal feathers not replaced in the first prebasic molt) in this presupplemental molt. Evidence that all first basic and remaining juvenal feathers are lost stems from (1) the color change in males from brown dorsally and buff-barred off-white ventrally to buff-tipped blue dorsally and buff-tipped blue, cinnamon, and white ventrally in males; (2) the discovery of three molting specimens (MCZ 16254, DEL 13141, CMNH 126489) with all three feather generations of body plumage which are clearly distinguishable by quality, wear, and color; and (3) the absence of the first two feather generations in the body plumage of all specimens that have completed the presupplemental molt.

Second, this second fall molt in Lazuli Buntings is undoubtedly homologous (*sensu* Humphrey and Parkes 1959) to the presupplemental molt described in Indigo and Painted Buntings (Rohwer 1986, Thompson 1991). In the latter two species, most or all of the body feathers are replaced once in the first prebasic molt and then again in the presupplemental molt. In Lazuli Buntings, the first prebasic molt has been reduced to a partial body molt, but the presupplemental molt has remained virtually unchanged as a complete body and rectrix molt and partial remex molt.

The nine specimens collected in this molt indicate it is completed between late September and early November. This molt progresses much more intensely than the first prebasic molt, with

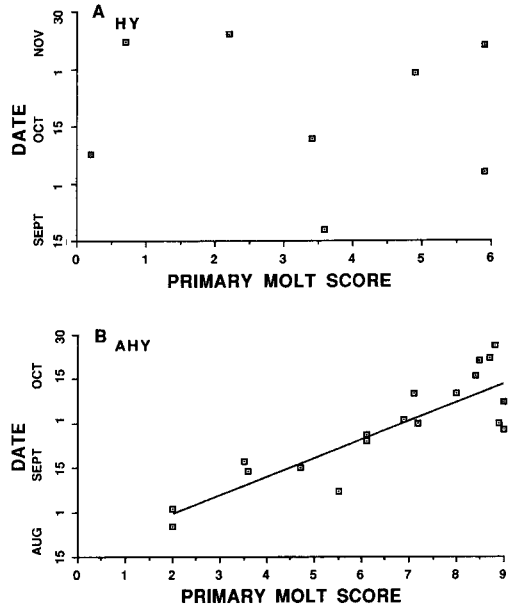


FIGURE 1. A) Attempt at estimating duration of primary replacement in presupplemental molt. There was no relationship between molt score and date. B) Regression of primary molt score on date for AHY adults. The relationship is described by the equation  $date = -6.82 + 6.32 (\text{molt score})$ .

an average molt score of 29.8 (range 1.7-66.7) for the eight specimens in body molt. Primary and secondary development proceeds in typical ascending order beginning with the third, fourth, or fifth primary (Table 2). Secondary development appears to begin with S8, continue with S7 and S9, and then either stop there or finish with S5 and S6 (Table 2). As Figure 1A shows, I was unable to estimate the duration of this molt in an individual bunting, suggesting that there is much between or within-year variation in when the molt occurs. In 23% of HY and SY specimens collected with grown supplemental plumage between 1 November and 30 April ( $n = 75$ ), one or more (mean 2.1, range 1-4) of the outermost primary coverts had also been replaced with adult-like feathers. In 29% of these cases, the molt was asymmetrical in that different numbers of primary coverts were replaced on the right and left wings.

*Prealternate molt.* The change in color from winter to breeding aspect comes about largely by wear of buff feather tips that exposes underlying colored vanes (Fig. 2). The prealternate molt is reduced to just a few feathers around the auric-

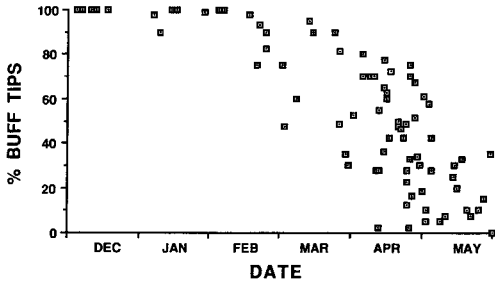


FIGURE 2. Wear of buff contour feather tips after the prebasic molt in AHY males.

ulars, eyes, and bill. A slightly more extensive molt can occur in SY males which also replace white throat feathers for buff-tipped blue feathers (see below). In all age classes, the new feathers are colored buff-tipped blue in males and brown in females. Because of the limited nature of the molt, the small size of the feathers involved, and the lack of color change, it was impossible to know by examining a specimen whether it had already molted. Thus, I cannot say whether all birds always undergo this molt. Molting birds were collected February through April, and there is some suggestion that ASY birds begin this molt earlier than SY birds (Table 3). Overall, 17.6% of the specimens collected from February through April were in molt. I cannot say whether the prealternate molt continues into May as is the case in SY Indigo Buntings (Rohwer 1986) because I did not examine May specimens for molt. Because it is so limited in extent, this molt does little to stem the gradual increase in feather wear that occurs from December through July (Fig. 3).

There were no statistically detectable differences between age and sex categories in the occurrence of prealternate molt (Table 3); however, the most intense prealternate molt scores found were in SY males, with up to 10% of throat feath-

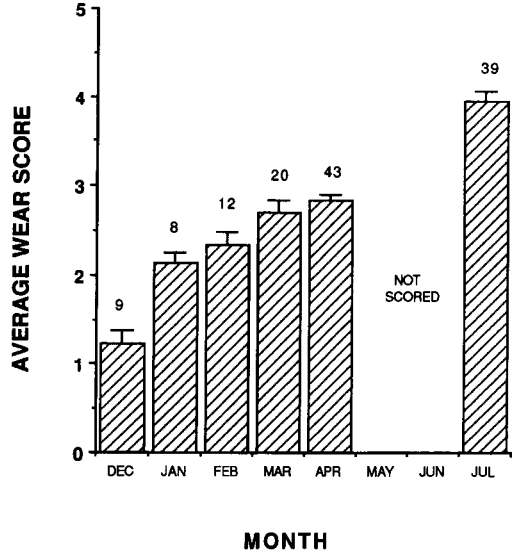


FIGURE 3. Wear of body feathers after the prebasic molt in ASY males and females. For the wear score, 1 = fresh and 5 = extremely worn. Monthly sample sizes indicated.

ers in development (e.g., MOORE 26867). During this molt, SY males lose many white throat feathers grown in during the presupplemental molt, making them appear significantly more similar to ASY males by the breeding season than in mid-winter. Before the molt (November to March), 64% of 28 specimens had white in the throat while just 36% of 33 SY males taken in July have white throat feathers (*G*-test of independence with William's correction,  $G_{adj} = 4.6714$ ,  $df = 1$ ,  $P < 0.05$ ). At this point, SY males differ only in having a duller blue or browner back, brown inner primaries and outer secondaries, and occasional white feathers in the throat.

*Definitive prebasic molt.* The prebasic molt into definitive plumage involves the replacement of all body and flight feathers. The majority of spec-

TABLE 3. Prealternate (PA) molt by age, sex class, and date for specimens taken February through April. The between-class differences in molt frequency are not significant (*G*-test of independence with William's correction,  $G_{adj} = 5.0255$ ,  $df = 3$ ,  $P > 0.1$ ; Sokal and Rohlf 1981).

	Age and sex class				Total
	SY-M	SY-F	ASY-M	ASY-F	
No. in PA molt	10	0	6	3	19
No. not in PA molt	33	8	49	18	108
Months in which PA molt was found	Apr.	—	Feb.-Apr.	Mar.	Feb.-Apr.

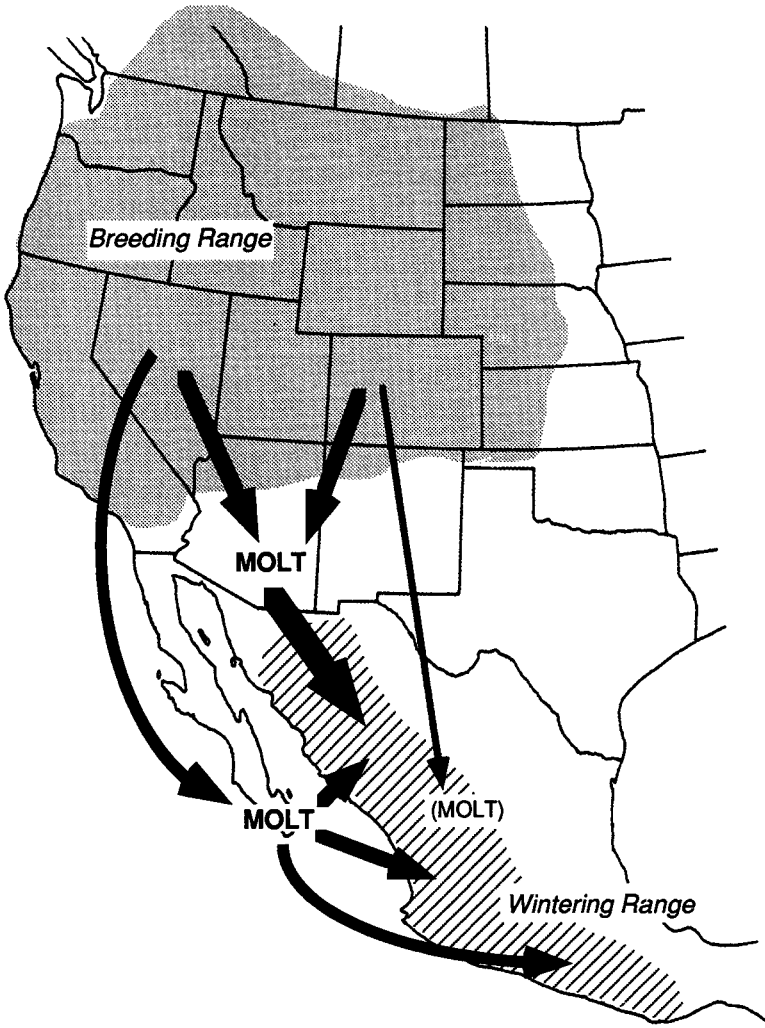


FIGURE 4. Geographical sequence of migration and molt events in the fall for Lazuli Buntings of all age and sex classes.

imens suggest that the body molt begins on the breeding grounds, is interrupted for migration, and then finishes concurrently with the prebasic wing and tail molt at a migratory stopover (Fig. 4).

In this molt, males change from worn blue to fresh buff-tipped blue dorsally and from worn blue, cinnamon, and white to buff-tipped blue, cinnamon, and white ventrally. Even the wing feathers have buff edges, especially the tertials (S7-9) and the feathers making up the wing bars. The resulting appearance is of overall buff that obscures the underlying bright blue and cinnamon colors. Adult males differ from subadult

males in that (1) definitive back feathers are brighter blue beneath their buffy tips and (2) chin feathers are almost never white. Females likewise change from worn breeding colors to fresh buff-tipped slate blue above and light brown below.

When the body molt begins on the breeding grounds, replacement occurs in all six regions. The molt intensity is light (Fig. 5B), and feather replacement is everywhere incomplete. Twenty-six percent of the 89 specimens from August and the first half of September taken on the breeding grounds or in southern Arizona and New Mexico had some fresh body feathers but were not in active molt (mean percent fresh feathers of those

with new feathers was 26.8). These individuals likely had halted molt for the southward migration which occurs at this time of year. The other specimens collected at this time were still in a light molt. As new flight feathers begin growing, the intensity of body molt increases and all remaining worn feathers are replaced. This is therefore not a presupplemental molt since feathers grown on the breeding ground are *not* replaced again when the rest of the body and flight feathers grow in. Body feathers of specimens in fresh basic plumage are in different wear classes indicating they were grown during different molting bouts.

The intensity of this part of the body molt is twice that of the breeding ground portion (Fig. 5B). The primaries and rectrices grow in the usual ascending manner. In the secondaries, the tertials (S7-9) are replaced first, simultaneous with the first primaries. The rest of the secondaries follow in ascending order beginning with S1. The rectrices grow in virtually synchronously, the outer feathers trailing the inner feathers by up to one-third of a grown feather-length. They initiate replacement soon after remigial replacement begins but are completed somewhat before the last primary and secondary are completed. The body molt is completed concurrently with the flight feather molt. A plot of collection date against molt score showed a significant regression ( $F_{1,17} = 53.109, P < 0.01, r^2 = 0.76$ ), and indicates flight feather molt lasts about 57 days (Fig. 1B). Caution is urged in interpreting this result since all sexes, AHY age classes, and locations were lumped to obtain an adequate sample size.

AGE AND SEX IDENTIFICATION

I found 21 male specimens collected in either April or July that had white feathers in the throat. Twenty (95.2%) were second year males. The one exception (MCZ 192432), collected in July, had about 10% of its throat feathers white and was certainly an ASY adult since it had all adult blue-edged black remiges and primary coverts. The throat feathers had not grown in white in the previous molt; instead, it appears that the blue portions of the feather vanes had completely worn away, exposing the basal white segments of the vanes.

I found no reliable external character to distinguish sexes in HY birds in juvenal or first basic plumage. Males and females were equally likely to have buff versus white or off-white wing bars (51% of 102 females had buff bars and 49% of

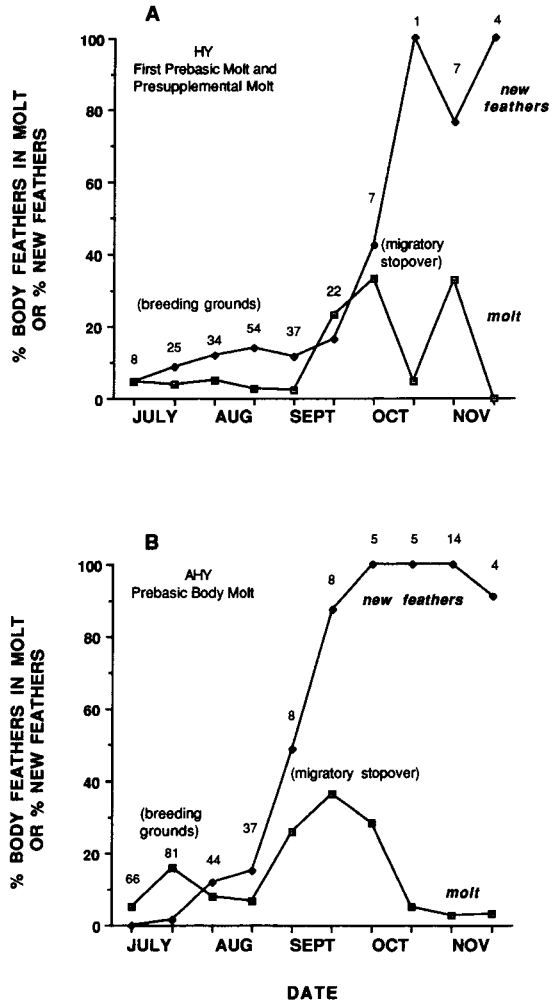


FIGURE 5. Molt intensity and feather replacement in HY (A) and ASY (B) buntings during the fall molts. Locations of the molts are indicated parenthetically. Numbers represent half-month sample sizes.

91 males had buff bars). I was less systematic about scoring rectrix color, but am nonetheless confident that this also is not reliable. At least ten of 102 females and nine of 91 males were noted with a blue rather than flat brown hue in their rectrices.

TIMING OF MIGRATION AND LOCATION OF FALL MOLTS

Figures 5-8 diagram the temporal and geographic occurrence of fall migration and molt in Lazuli Buntings. HY birds linger on the breeding grounds until September when they begin to appear in



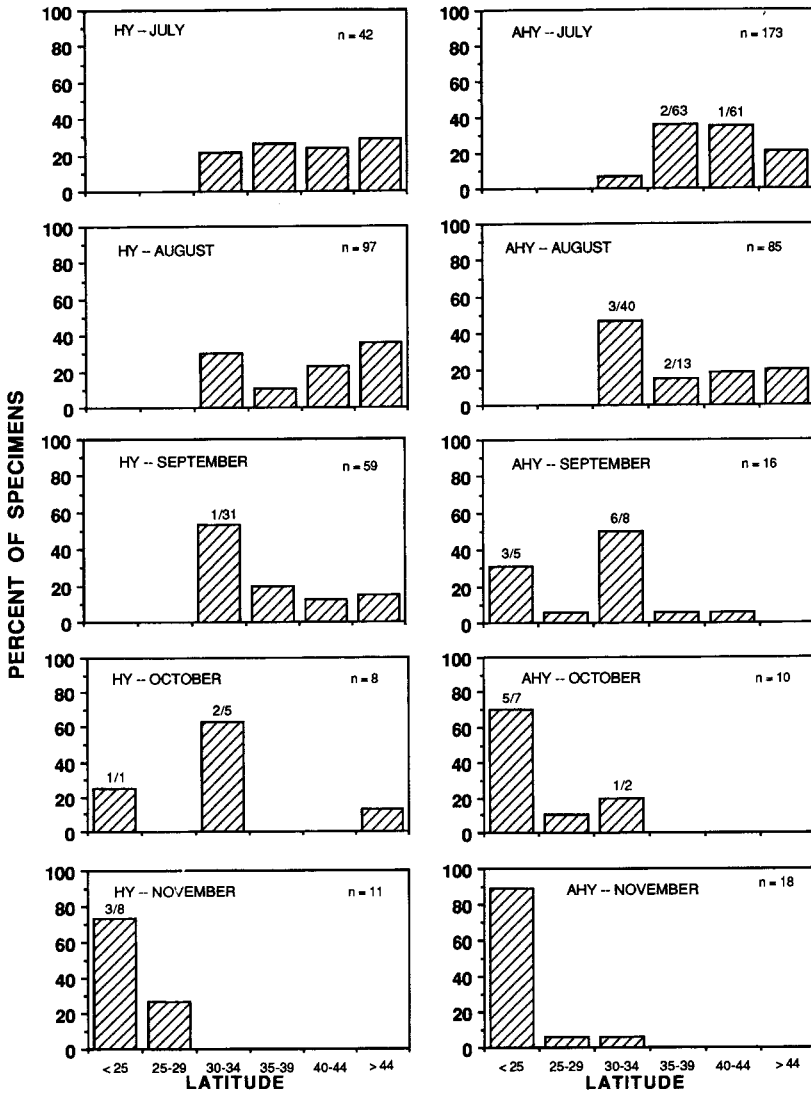


FIGURE 6. Locations of HY (left) and AHY (right) specimens before, during, and after the fall molts. Figures above the bars are the number of specimens in flight feather molt/total number of specimens for a latitude region where there were  $\geq$  one specimen in molt. 30–34° corresponds to the southwestern U.S./northern Sonora region and <25° represents both southern Baja California and western Mexico.

the southwestern U.S./northern Sonora (SWUS/NS) region. Here they stay into October before traveling south to the wintering grounds in western Mexico (WM). Some also visit southern Baja California (SBC); whether they do this in lieu of stopping in SWUS/NS or after stopping there cannot be determined. AHY adults depart the breeding grounds sooner than HY birds, arriving in the SWUS/NS by late August and early Sep-

tember (Fig. 6). Again, some fly to SBC either directly, or possibly via SWUS/NS. All AHY birds then arrive on the wintering grounds by November.

In HY birds, the first prebasic molt occurs on the breeding grounds in June, July, and August (Table 1) and is then followed by a nearly complete presupplemental molt in late September, October, and early November (Figs. 5–6). The

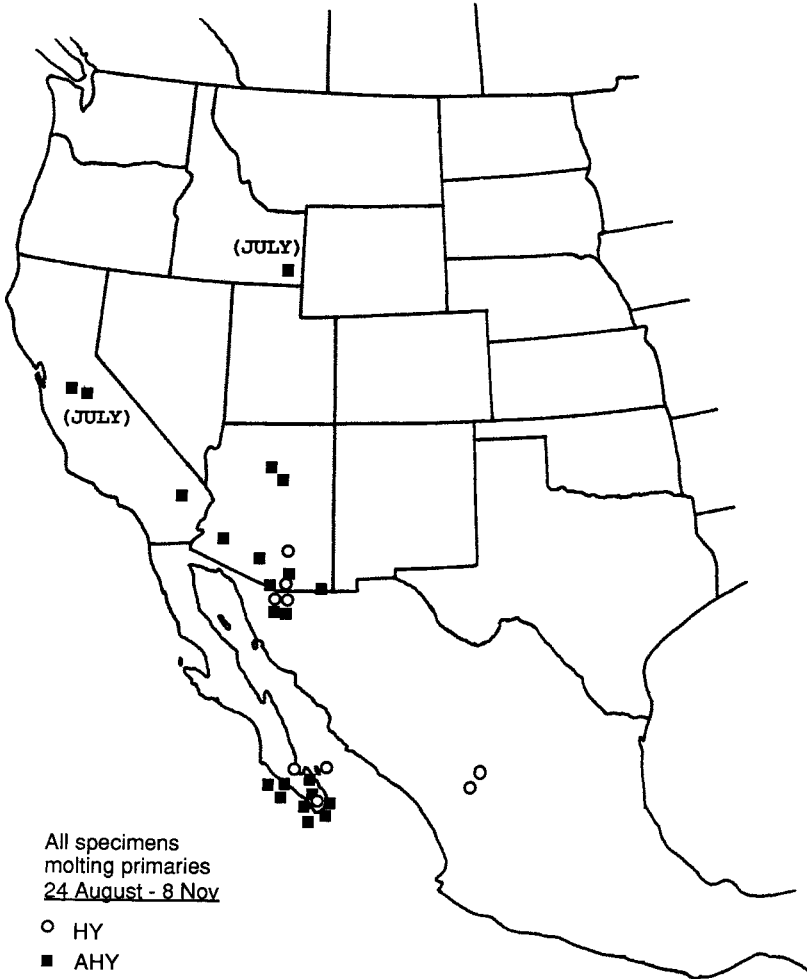


FIGURE 7. Locations and age classes of all specimens molting flight feathers; all specimens were collected between 24 August and 8 November except as noted.

presupplemental molt occurs primarily in the SWUS/NS and SBC, although two specimens (DEL 13141 and DEL 13142) were in presupplemental molt in Durango, WM (Fig. 7). AHY birds begin the body molt on the breeding grounds, then finish the body molt and undergo the entire flight feather molt in the same SWUS/NS and WM regions, but earlier. No AHY specimen was found in molt in WM, although two specimens from this region, an ASY male (KU 30164) and a SY female (MOORE 6201), were found in worn flight and body feathers indicating they were likely to molt in this region (Fig. 8). Thus there are four steps to the usual fall migration/molt sequence (Fig. 4): (1) a partial body

molt (the entirety of the first prebasic molt in HY, and part of the definitive prebasic body molt in AHY birds) on the breeding grounds; (2) a migration to SWUS/NS or SBC; (3) a continuation of a molt that finishes body feather replacement and replaces all flight feathers (i.e., finish definitive prebasic molt in AHY birds) or a complete body molt and a partial flight feather molt (presupplemental molt in HY birds); and (4) a migration to the wintering grounds in WM.

Evidence for this fall molt-migration sequence comes from five observations. First, some body molt clearly occurs on the breeding grounds (Fig. 5). Second, Figure 7 shows that virtually all specimens in flight feather molt were collected out-

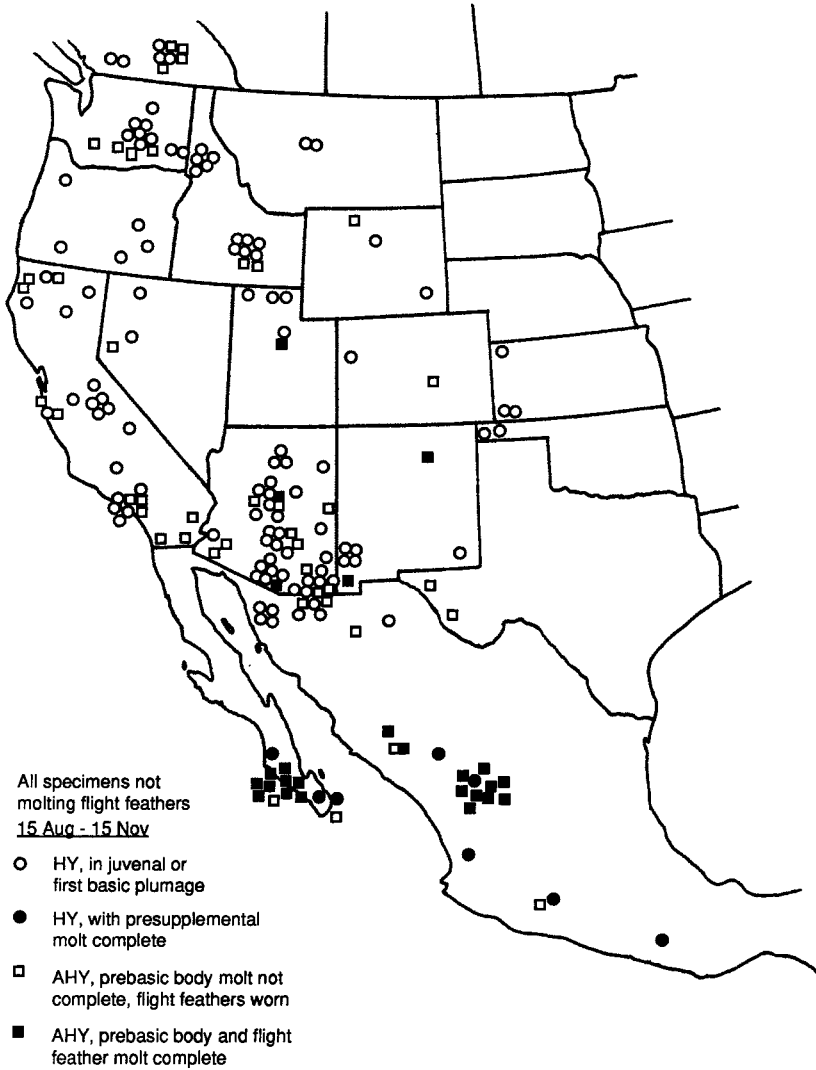


FIGURE 8. Locations, age classes, and plumages of all specimens collected 15 August to 15 November not in flight feather molt.

side of the breeding range. This is not due to a bias in collecting effort since many specimens not molting flight feathers were taken from the breeding range during this period (Fig. 8). Third, many individuals were collected south of the breeding grounds in worn plumage (Fig. 8). Fourth, the occurrence of specimens in flight feather molt is skewed to two areas, the SWUS/NS and SBC (Fig. 7). Specimens from WM were scarce, so I cannot rule this area out as a third major site of molting. Finally, the two molting “hotspots” are out of the normal winter range

(Table 4), indicating that buntings arrive, molt, and then depart the two molting regions.

In exception to this scheme of migrating before finishing the fall definitive prebasic molt, I found three specimens from the breeding range in advanced body and wing molt (Fig. 7), a SY male (MVZ 80401), an ASY male (MVZ 80400), and an ASY female (UMMZ 75828). These three are from July whereas all other specimens at this stage of the prebasic molt were collected from late August through October. I suspect these three failed at breeding and underwent a full molt

TABLE 4. Occurrence of specimens in all age and sex classes at the major molting regions before, during, and after the major fall molt.

Date	Southern U.S./ northern Sonora	Southern Baja California	Western Mexico	n
July (before molt)	100 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>	7
15 Aug–15 Nov (during molt)				
Total	63	20	17	115
Actually molting flight feathers	50	43	7	28
Dec–Mar (after molt)	8	6	86	77

<sup>a</sup> Values represent percentage of total specimens collected in each time period.

in lieu of caring for offspring. Several studies show that unsuccessful breeders, often yearlings, molt earlier than successful breeders (Payne 1972, Bancroft and Woolfenden 1982, Rimmer 1988).

## DISCUSSION

### WHY INTERRUPT MIGRATION?

Despite an extensive literature search, I could find just three additional reports of passerines interrupting migration to molt: Bullock's Oriole and Painted Bunting in the SWUS/NS (Rohwer and Manning 1990, Thompson 1991) and Eurasian Yellow-breasted Bunting in Asia (Stresemann and Stresemann 1966). Among non-passerines, waterfowl are well-known to take special molt migrations after breeding, but finding a safe place to be flightless during the molt seems to be a more important factor than finding food in waterfowl.

Rohwer and Manning (1990) suggested that Bullock's Orioles migrate out of their western North American breeding grounds in the fall to escape food scarcity brought on by predictable late summer droughts (see Baldwin 1973). Bullock's Orioles molt in the southwestern U.S./northern Sonora region where they may be taking advantage of the food flush caused by scattered late summer rains (Shreve and Wiggins 1964, Ezcurra and Rodrigues 1986, Neilson 1986). Likewise, most Painted Buntings from the drier, western portion of their breeding range migrate to the SWUS/NS or Rio Grande valley in the fall. Here they perform their complete fall molt and then resume their migration to their southern Mexico wintering grounds (Thompson 1991). The factors causing both Bullock's Orioles and Painted Buntings to interrupt their migration for molting are likely to be similar to those acting on Lazuli Buntings since all breed in areas with similar climates and all molt in the same geo-

graphical areas. Further supporting this resource-based explanation is the observation that southern Baja California, the second major molting area for Lazuli Buntings, also receives its rain in the late summer (Wiggins 1980) and likely also has abundant food at this time.

A possible difficulty with this scenario, though, is that Lazuli Buntings occur in association with either riparian habitats or irrigated agricultural areas (Erickson 1968). One might not expect these habitats to undergo such drastic late summer food shortages that would cause buntings to leave without finishing their molt. Until further information is available on food abundance in the breeding and molting areas, we cannot be sure of the basis for the fall molting/migration pattern seen in Bullock's Oriole and Lazuli Bunting.

Nonetheless, three passerines have now been documented to molt in the southwestern U.S./northern Sonora region. Many other species are known to migrate through these areas as well; examination of museum specimens of these species collected in the SWUS/NS in September and October may show that even more species molt in this region than are presently recognized. These yet unidentified species and Lazuli Buntings thus have a conservation problem akin to shorebirds and waterfowl in needing preservation of winter, breeding, and migratory habitats for complete protection.

### BETWEEN SPECIES COMPARISONS

It is remarkable that the three well-studied and presumably closely related *Passerina* buntings are so different in extent and timing of molt relative to migration (Table 5). The three species differ in extent of the first prebasic molt, timing of the presupplemental molt relative to migration, color change of the presupplemental molt with respect to adult color, extent of the prealternate

TABLE 5. A comparison of molt and plumage characters for Painted Bunting, *Passerina ciris* (Thompson 1991), Indigo Bunting, *P. cyanea* (Rohwer 1986), and Lazuli Bunting, *P. amoena* (this study).

Molt	Species	Time	Location <sup>1</sup>	Extent of feather replacement	Color change
First prebasic	<i>ciris</i>	Jun–Oct	BG	most body	to brighter green
	<i>cyanea</i>	Jun–Oct	BG	all body	to slightly browner
	<i>amoena</i>	Jun–Sep	BG	some–most body	to buff breast bar
Presupplemental	<i>ciris</i>	Sep–Nov	BG <sup>2</sup> or migratory stopover	all body, P6, 7, or 8–P9, S5, 6, or 7–S9	to adult female-like
	<i>cyanea</i>	Nov–Dec	WG <sup>3</sup>	all body, P4, 5, 6–P9, S7–S9	M: to scaly blue F: no change
	<i>amoena</i>	Sep–Nov	migratory stopover or WG	all body, P3, 4, 5–P9, S5, 6, 7–S9	M: to male-like F: to female-like
First prealternate	<i>ciris</i>	Dec–May	WG	some to all head; some body	none
	<i>cyanea</i>	Feb–May	WG	some to all body	M: to male spring blue F: none
	<i>amoena</i>	Apr	WG	throat, some head	M: to male blue F: none
Definitive prebasic	<i>ciris</i>	Aug–Nov	BG or migratory stopover	complete	M: to bright male F: to female
	<i>cyanea</i>	Aug–Sep	BG	complete	M: to scaly blue F: to female
	<i>amoena</i>	Jul–Oct	begin on BG, finish in migratory stopover or WG	complete	to buff-tipped adult colors
Second and subsequent prealternate	<i>ciris</i>	Jan–May	WG	some to all head; some body	none
	<i>cyanea</i>	Jan–Apr	WG	all body	M: to spring blue F: none
	<i>amoena</i>	Feb–Apr	WG	few head	none

<sup>1</sup> BG = breeding grounds, WG = wintering grounds.

<sup>2</sup> A few individuals were found to undergo this molt on the wintering grounds.

<sup>3</sup> A few individuals were found to undergo this molt on the breeding grounds.

molt, location of the definitive prebasic molt, and mode of color change from winter to breeding aspect. Because the three species are largely allopatric, it is likely that different social, predatory, and food conditions may have led to the evolution of the different molt strategies. For these three species, we have reached the limit of what museum specimens can tell us. To identify which are the most important factors influencing molt evolution, we will need field observation and experimentation. In light of this study and those on other *Passerina* buntings (Rohwer 1986, Thompson 1991), it would be presumptuous to generalize as Pyle et al. (1987) did about similar molt pattern followed by members of the genus except for the names of the molts and the general time of year in which they occur. Interestingly, Rohwer and Manning (1990) found that the closely related Bullock's and Baltimore Orioles, presently considered a single species, resemble

buntings by differing in the extent of the prealternate molt and in the timing of the prebasic molt relative to migration. Furthermore, Rohwer and Manning (1990) showed that hybrids between the two oriole forms can have maladaptive molt patterns. Emlen et al. (1975) found few Lazuli × Indigo hybrids and speculated that these were at some sort of selective disadvantage. Assuming that timing relative to migration and extent of molt are under genetic control, a mechanism for strong selection against hybrids of any two *Passerina* species (e.g., Sibley and Short 1959, Storer 1961) may be maladaptive intermediate molt patterns.

Inspection of Table 5 shows that the three *Passerina* species often display features at different points along several character continua. *Passerina amoena* often falls at the extremes of the character states, having the most reduced prealternate molt, replacing the most primaries in the

presupplemental molt, replacing the fewest feathers in the first prebasic and prealternate molts, and appearing the most adult-like after the presupplemental molt. Whether this represents a derived or ancestral condition with respect to the other species cannot be determined without a good phylogeny of the group. The variation among *Passerina* species in extent, timing, and geographic location (relative to breeding and wintering ground) of molts would never have been predicted from their apparent close relationships. A good molecular phylogeny for the entire genus and its closest relatives might clarify the sequence of evolutionary changes and strategies. Either Painted, Lazuli, and Indigo Buntings are less closely related than earlier work has suggested or many aspects of molting are evolutionarily more labile than conventional wisdom has admitted. If the latter is true, then the genus *Passerina* holds the potential for being the first group of birds for which the direction of change in molt patterns (in a variety of aspects of molt) could be deduced from a good phylogeny.

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