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## THE SEQUENCE OF MOLTS AND PLUMAGES IN PAINTED BUNTINGS AND IMPLICATIONS FOR THEORIES OF DELAYED PLUMAGE MATURATION<sup>1</sup>

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**Abstract.** Within a week of fledging, juvenile Painted Buntings, *Passerina ciris*, undergo a previously unrecognized first prebasic molt that includes most to all body plumage except greater primary and greater secondary coverts. This molt occurs from early June to early October, usually on the breeding ground. The resulting first basic plumage is similar to juvenal plumage, but is more adult female-like in color in both sexes. First-year, but not adult, Painted Buntings subsequently undergo a presupplemental molt during which the outer four or five primaries, inner four to six secondaries, all remiges, and all body plumage except some to all greater primary coverts typically are replaced. The resulting supplemental plumage is identical in both sexes and is more adult female-like in color than the previous first basic plumage. Presupplemental molt usually occurs between early September and early November. Most (90%) Painted Buntings along the eastern coast of the United States undergo this molt on the breeding ground prior to fall migration; whereas, in the western United States, most (60%) molt in exclusively migratory areas of the desert southwestern United States and northwestern Mexico. These desert locations exhibit a large increase in plant and insect life in response to "monsoon" rains that occur predictably in these areas in late summer and fall. Selection may have favored evolution of molt-migration strategies in Painted Buntings in the western United States as a mechanism to allow them to molt in areas with greater food resources than exist at the same time of year on their breeding or wintering ground. Painted Buntings are one of only six passerines in which molt-migration has been documented.

All age and sex classes undergo a partial prealternate molt that was described previously (Fisk 1974) but has been overlooked by all subsequent investigators. This molt usually occurs on the wintering ground, and is typically limited to the head, breast, and belly. Most plumage grown by subadult males during first prealternate molt is adult female-like in color. This is the only passerine known in which sexually mature subadult males grow adult female-like rather than adult male-like plumage during prealternate molt.

Juvenal plumage has poor structural integrity compared to subsequent plumages. Its structure facilitates heat transfer to the young by brooding females, but is poorly adapted to protecting juveniles from adverse effects of abiotic factors. Therefore, selection may have favored replacement of juvenal plumage with a structurally stronger first basic plumage as soon as possible after fledging.

First-year males and females may undergo presupplemental molt to prevent being identified as first-year birds by adult females and being dominated by them (and possibly by adult males as well if adult males do not usually dominate adult females), or to reduce predation on themselves. That no subadult males acquire a winter plumage intermediate in color between that of adult males and adult females in winter is the first empirical support for Rohwer et al.'s (1980) model which indicates that selection should favor subadult males with plumages that are completely adult female-like or adult male-like more than plumages that are intermediate between adult males and adult females. These results also support the winter female mimicry hypothesis (Brown and Brown 1988), are consistent with the winter

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cryptic hypothesis (Rohwer and Butcher 1988), and are inconsistent with the winter status signaling hypothesis (Rohwer 1975, 1982).

Because subadult males grow plumage during first prealternate molt that is adult female-like in color, this strongly suggests that the resulting plumage functions during their first potential breeding season to mimic females. This supports the summer female mimicry hypothesis (Rohwer et al. 1980), but is inconsistent with the summer cryptic (Selander 1965, 1972), summer status signaling (Lyon and Montgomerie 1986, Montgomerie and Lyon 1986) and juvenile mimicry hypotheses (Lawton and Lawton 1986, Foster 1987). This also supports Rohwer et al.'s (1980) model discussed above.

Adult males exhibit a greater rate of feather replacement during prealternate molt than any other age or sex class. This suggests that the extent of this molt is less constrained in adult males than other age and sex classes, thus weakly supporting the molt constraints hypothesis (Rohwer and Butcher 1988).

Because subadult males exhibit only a limited prealternate molt, their summer plumage may not be functionally independent of their winter plumage. Thus, it is not possible to conclusively determine whether subadult male plumages are adaptive during winter, summer, or both. Because presupplemental body molt is essentially complete, this clearly indicates that failure of subadult males to obtain fully adult male-like supplemental plumage can not be due to energetic constraints.

*Key words:* Molt migration; delayed plumage maturation; Passerina; museum specimens; color; energetics; constraints.

## INTRODUCTION

In nearly all species of birds, females reach sexual and somatic maturity at the same time (but see Ligon 1971, Hussell 1983, Stutchbury and Robertson 1987, Mountjoy and Robertson 1988). However, males of many species do not attain somatic maturity in plumage or bare part color for months to years after reaching sexual maturity. In sexually mature but somatically immature (subadult *sensu* Rohwer et al. 1980, Rohwer and Butcher 1988) males, these characters are more cryptic than those in adult males (Rohwer et al. 1980, Lawton and Lawton 1986, Butcher and Rohwer 1989) and usually are very similar to those of adult females. In many of these species subadult males successfully breed occasionally to regularly (e.g., Diamond 1972, Forshaw and Cooper 1981, Proctor-Gray and Holmes 1981, Steenhof et al. 1983, Goodwin 1986, Grant 1986, Lawton and Lawton 1986, Rohwer and Butcher 1988). Such delayed acquisition of adult plumage by sexually mature birds is termed delayed plumage maturation. Delayed plumage maturation has been studied almost exclusively in North American passerines (but see Foster 1987, Järvi et al. 1987), but its occurrence is geographically and taxonomically more widespread than is generally recognized. It occurs in at least seven orders and 11 families of non-passerines and at least 21 families of passerines (e.g., Mayr 1933, 1934; Lack 1968; Diamond 1972; Forshaw and Cooper 1981; Schodde 1982; Grant 1986; Lawton and Lawton 1986; Rohwer and Butcher 1988), including species that are sex-

ually monochromatic and dichromatic, that have a variety of mating systems and migratory strategies, and that occur throughout the world in diverse habitats ranging from arctic tundra at high latitudes to tropical rain forests at low latitudes.

All hypotheses for the evolution of delayed plumage maturation propose that the relatively cryptic plumage of subadult males is adaptive either during their first non-breeding season (winter hypotheses) or their first potential breeding season (summer hypotheses). The function of plumage color during breeding season (usually summer) may be considered independent of plumage color during nonbreeding season (usually winter) only when a complete body molt occurs between these seasons (Rohwer 1986, Rohwer and Butcher 1988, Butcher and Rohwer 1989).

Although most studies of delayed plumage maturation have argued that subadult plumages evolved as adaptations for breeding, Rohwer and Butcher (1988) elegantly and unambiguously demonstrated that subadult plumages often are adaptive only in winter. Males of 16 species wear subadult plumages only during their first winter. In all of these species, subadult males undergo a complete body molt in spring which causes them to lose their adult female-like winter plumage and acquire a summer plumage that is very similar or identical to that of adult males. This indicates that subadult plumage in these species must be an adaptation to winter.

Males of 21 species wear subadult plumage

during their first winter and subsequent summer. In all of these species, subadult males undergo a limited spring body molt thereby acquiring a more adult male-like plumage. Because this molt is incomplete, summer plumage may not be functionally independent of winter plumage. Therefore, this finding does not unequivocally support either winter or summer hypotheses. All plumage replaced during spring molt in these 37 species is always adult male-like and never adult female-like or cryptic (Rohwer and Niles 1979, Rohwer et al. 1983, Rohwer 1986, Rohwer and Butcher 1988).

Fourteen species of North American passerines have equally cryptic winter and summer subadult male plumages (Table 1, category 3 in Rohwer and Butcher 1988). Because there is no evidence of a spring molt in any of these species, Rohwer and Butcher (1988) explicitly assume that these species do not change plumage color from winter to summer because they lack a spring molt. However, only one of these species, the Northern Oriole, *Icterus galbula* (Rohwer and Manning 1990), has been specifically investigated for the occurrence of a spring molt. Evidence that subadult males of any of these species replace a cryptic winter plumage with either an equally or more cryptic or a more adult female-like summer plumage during a complete spring body molt would clearly demonstrate, in the species in question, that it is more adaptive for them to wear subadult male than completely adult-male-like plumage in summer. If the spring body molt is incomplete, this does not necessarily indicate that it is more adaptive for them to wear subadult male than completely adult-male-like plumage in summer, but may indicate that it is more adaptive to wear a subadult plumage that is completely adult female-like rather than intermediate in color between adult females and males (Rohwer et al. 1980, 1983; Rohwer and Butcher 1988).

I initiated this study to determine whether a spring molt occurs in one of these 14 species, the Painted Bunting, *Passerina ciris*. Subadult male Painted Buntings are very cryptic in color and exhibit the least change in plumage color from winter to summer compared to subadult males of the other 13 species. In addition, subadults of congeneric Indigo Buntings, *Passerina cyanea*, undergo a spring molt of some to all body plumage, except greater primary coverts (Rohwer 1986). This suggests that Painted Buntings may exhibit a similar molt. Therefore, Painted Bun-

tings are an ideal choice of species in which to look for a spring molt. In addition, three winter and five summer hypotheses imply testable predictions regarding subadult male molts and plumages. These predictions were tested by determining the sequence of molts and plumages, and resulting changes in plumage color, exhibited by male Painted Buntings from hatching to somatic maturity. The relevant winter and summer hypotheses are summarized below. The predictions of these hypotheses are summarized in Table 1 and explained in the discussion.

All winter and summer hypotheses assume that competition is intense among age classes of males during winter and summer, respectively. Less experienced subadult males are presumably competitively disadvantaged relative to older males. All of these hypotheses, except the breeding threshold hypothesis (Studd and Robertson 1985, Montgomerie and Lyon 1986), also propose that delayed plumage maturation has evolved in subadult males either to reduce predation or to reduce aggression directed toward them by adult males, and differ only in the proposed proximate mechanisms by which subadult males reduce aggression directed toward them. The breeding threshold hypothesis is an extension of theory developed by Wiley (1974, 1981) and Wittenberger (1978, 1979), and is not addressed by this study because it makes no testable predictions regarding seasonal changes in plumage color and does not invoke a specific adaptive proximate function to subadult plumage. Instead, it argues that selection for reduced male-male competition has favored the evolution of subadult plumage and increased body size in birds that experience intense male-male competition.

#### WINTER HYPOTHESES

The *winter status signaling hypothesis* (Rohwer 1975, 1977, 1978a, 1982, 1985; Rohwer and Rohwer 1978; Ketterson 1979; Rohwer and Ewald 1981; Rohwer and Butcher 1988) states that plumage color functions intraspecifically to honestly signal dominance rank within social groups, conspicuous color being dominant to more cryptic color. Status signals may also function to indicate inherent cost-benefit asymmetries among group members (Parker 1974, Maynard Smith and Parker 1976, Ewald and Rohwer 1980).

The *winter cryptic hypothesis* (Ewald and Rohwer 1980, Rohwer et al. 1983, Rohwer 1986, Rohwer and Butcher 1988) proposes that the rel-

TABLE 1. Seasonal changes in plumage color in subadult male Painted Buntings and their implications for winter and summer hypotheses for the evolution of delayed plumage maturation (DPM).

Name of Hypothesis	Possible changes in plumage color in first-year males in any species with DPM from summer to winter <sup>1</sup> that would support (S), be consistent with (C) or be inconsistent with (I) the hypothesis. Observed change in first-year male Painted Buntings is italicized	Possible changes in plumage color in subadult males in any species with DPM from winter to summer that would support (S), be consistent with (C) or be inconsistent with (I) the hypothesis. Observed change in subadult male Painted Buntings is italicized
Winter Status Signaling	More male-like (S) No change (C) <i>More female-like (I)</i>	More male-like (C) <i>No change (C)</i> More female-like (S)
Winter Cryptic	<i>More conspicuous (I)</i> No change (C) Less conspicuous (S)	More conspicuous (C) <i>No change (C)</i> Less conspicuous (I)
Winter Female Mimicry	More male-like (I) No change (C) <i>More female-like (S)</i>	More male-like (C) <i>No change (C)</i> More female-like (I)
Summer Status Signaling	No predictions	Less female-like (S) <i>No change<sup>4</sup> (C,<sup>2</sup> I<sup>3</sup>)</i> More female-like (I)
Summer Cryptic	No predictions	More conspicuous (I) <i>No change<sup>4</sup> (C,<sup>5</sup> I<sup>6</sup>)</i> Less conspicuous (S)
Summer Female Mimicry	No predictions	Less female-like (I) <i>No change<sup>4,8</sup> (I,<sup>6</sup> S<sup>7</sup>)</i> More female-like (S)
Juvenile Mimicry	No predictions	Less juvenile-like (I) <i>No change<sup>4</sup> (S,<sup>9</sup> I<sup>10</sup>)</i> More juvenile-like (S)
Molt Constraints	No predictions	No predictions

<sup>1</sup> Change in plumage color from summer to winter may result from first prebasic molt, presupplemental molt, feather wear, or a combination thereof.  
<sup>2</sup> No change in plumage color would be consistent with this hypothesis only if subadult male winter plumage color is intermediate between that of adult males and females, which is not the case in Painted Buntings.  
<sup>3</sup> No change in plumage color would be inconsistent with this hypothesis if subadult male winter plumage color is completely adult female-like, as occurs in Painted Buntings.  
<sup>4</sup> 43% of subadult male Painted Buntings grow some adult male-like (blue) head plumage during first prealternate molt (see Table 2).  
<sup>5</sup> No change in plumage color would be consistent with this hypothesis only if subadult male winter plumage color is maximally cryptic, which is not the case in Painted Buntings.  
<sup>6</sup> No change in plumage color would be inconsistent with this hypothesis only if subadult male winter plumage color is not completely adult female-like, which is not the case in Painted Buntings.  
<sup>7</sup> No change in plumage color would support this hypothesis only if subadult male winter plumage color is completely adult female-like, as occurs in Painted Buntings.  
<sup>8</sup> Because subadult male and female Painted Buntings are identical in plumage color in winter, it is not possible for subadult males to become more adult female-like in plumage color in summer.  
<sup>9</sup> No change in plumage color would support this hypothesis only if subadult male winter plumage color is completely juvenile-like, which is not the case in Painted Buntings.  
<sup>10</sup> No change in plumage color would be inconsistent with this hypothesis if subadult male winter plumage color is not completely juvenile-like, as is the case in Painted Buntings.

actively cryptic plumage of subadults reduces their conspicuousness to both predators and conspecific adult males during their first winter.

The *winter female mimicry hypothesis* (Brown and Brown 1988) suggests that, in species in which adult males preferentially allow females access to resources, subadult males with adult female-like 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 an adult female-like plumage that deceives adult males into identifying them as females and behaving subordinatesly toward them. For this hypothesis to explain subordinate

behavior of males to many or all adult females other than their mates and to subadult males in adult female-like plumage, one must assume 1) that reciprocal altruism (Trivers 1971) exists among males toward these females or 2) that by doing so, males may increase their probability of pairing and/or mating with these females in the future.

SUMMER HYPOTHESES

The *summer status signaling hypothesis* (Lyon and Montgomerie 1986, Montgomerie and Lyon 1986) proposes that subadult male plumage color is a reliable signal of fighting ability rather than

a deceitful indicator of sex. It requires that 1) male-male competition is intense due to a strongly male-biased operational sex ratio, 2) females choose mates based on intrinsic male attributes such as plumage color, but not on extrinsic cues such as territory quality, and 3) subadult males have "lower intrinsic resource holding potential than adult [males]" which precludes them from winning territorial contests with adult males. It argues that when these conditions obtain, subadult males do not pose a threat to adult males and, therefore, should be tolerated by them.

The *summer cryptic hypothesis* (Selander 1965, 1972; Lack 1968; Proctor-Gray and Holmes 1981) assumes that the primary function of conspicuous color is to increase success in male-male competition for breeding resources, but that conspicuous color also increases predation and/or intraspecific competition relative to more cryptic color. It also assumes that, on average, subadult males that attempt to breed during their first potential breeding season achieve lower reproductive success than breeding adult males. Last, it argues that the relatively higher reproductive success that may be gained by subadult males in more adult male-like than adult female-like breeding plumage is outweighed by their proportionally higher mortality than subadult males in more adult female-like breeding plumage.

The *summer female mimicry hypothesis* (Rohwer 1978b, 1983; Rohwer and Niles 1979; Rohwer et al. 1980, 1983) is based on the premise that adult males minimize aggression toward females during breeding season to facilitate pair-bonding and extra-pair copulations. It asserts that adult female-like breeding plumage in subadult males is adaptive. For a short time after arrival on the breeding ground, subadult males behave cryptically. As a result, adult males mistake subadult males for females for a sufficient time for subadult males to establish site dominance and gain breeding territories capable of attracting reproductive females. This strategy should increase both survivorship and reproductive success of subadult males.

An alternative explanation for female mimicry is that selection may favor "males to allow females access to critical resources that may be channeled into the production of eggs and young, in which males have genetic interest" (Brown 1984). Subadult males may exploit this relationship between adult males and females by wearing an adult female-like plumage that deceives adult males into identifying them as females and be-

having subordinately toward them, thereby increasing access to food by subadult males. For this hypothesis to explain subordinate behavior of males to many or all adult females other than their mates and to subadult males in adult female-like plumage, one must assume 1) that reciprocal altruism (Trivers 1971) exists among males toward these females or 2) that by doing so, males may increase their probability of pairing and/or mating with these females in the future.

The *juvenile mimicry hypothesis* (Lawton and Lawton 1986, Foster 1987) proposes that 1) juvenile rather than female-like morphological and behavioral characteristics are retained by subadult males during their first potential breeding season, and 2) adult males display less aggression toward subadult than adult males because subadult males exhibit juvenile-like rather than female-like or adult male-like characteristics. Foster (1987) further asserts that retention of juvenile-like characteristics during the breeding season by sexually mature subadult males deceitfully signals nonreproductive status, whereas Lawton and Lawton (1986 and pers. comm.) maintain that retention of such juvenile-like characters could act either as deceitful signals of age or as honest signals of subordination.

The *molt constraints hypothesis* (Rohwer 1986, Rohwer and Butcher 1988) proposes that subadult males are unable to attain adult breeding plumage by their potential breeding season because of either 1) an inability to acquire sufficient resources to supply the energy for a late winter or spring molt or 2) genetic constraints that have prevented the evolution of a late winter or spring molt unique to subadult males (Parkes 1967). Cryptic plumages worn by subadult males during their first potential breeding season are, therefore, viewed as maladaptive.

Last, if subadult males do not replace all of their body plumage during a prebreeding molt in late winter or spring, then their winter and summer plumages may not be functionally independent. In such cases, no definite conclusions can be made regarding the season to which subadult male plumages are adapted.

## METHODS

The data for this study were collected from live specimens examined during a field study of this species at McKinney Falls State Park (30°11'28"N, 98°43'19"W), Travis County, Texas from May through July, 1984, and over 2,600

museum skins collected during all months of the year from throughout their breeding and wintering ranges. All museum skins were examined under a 100-W incandescent light with a 3.5× jeweler's optiviser.

#### SCORING MOLT

Terminology regarding names of molts and plumages follows Humphrey and Parkes (1959). The presence of molting feathers was determined by lifting the feathers with forceps. The intensity of body molt was scored separately on the crown, chin and throat, face (auricular region, ocular region, and lores), back, rump, breast, and belly. Definitions of body regions follow Rohwer (1986). Following Rohwer (1986), the intensity of body molt in each region was scored as follows: 0 = no new feathers, 10 = 1–20% new feathers, 30 = 21–40%, . . . 90 = 81–99%, 100 = body molt completed. To avoid mistaking adventitious molt for true molt, I assigned molt scores of 0 to specimens showing less than five growing feathers in only a single body region. Specimens with at least two growing feathers in each of two or more body regions were considered to be in molt. The total percentage of growing feathers on each specimen was estimated by calculating the average of the molt scores for the forehead, crown, nape, face, and chin and throat regions, and is hereafter referred to as total body molt score. In analyses of prealternate body molt, body molt scores were used for areas on the head only because of the rarity of observing prealternate body molt in other body regions on museum specimens (see discussion below). In addition, the location and extent of blue and red plumage was noted for all females and subadult males.

Flight feathers were scored on the following scale modified from Ginn and Melville (1983): 0 = old feather, 1 = missing feather, 2 = new feather less than  $\frac{1}{3}$  grown, 3 = new feather greater than  $\frac{1}{3}$  grown and less than  $\frac{2}{3}$  grown, 4 = new feather greater than  $\frac{2}{3}$  grown and less than full grown, 5 = new feather full grown and unshathed. Molting flight feathers were identified by their symmetrical loss and replacement. Only feathers in molt, as opposed to feathers lost or replaced adventitiously, were counted. Total primary, secondary, and rectrix molt scores were calculated by summing molt scores for individual primaries (P) from both wings, secondaries (S) from both wings, and all rectrices, respectively. Total flight feather molt score was cal-

culated by summing total primary, secondary, and rectrix molt scores. Painted Buntings have 18 primaries, 18 secondaries, and 12 rectrices. Adults replace all flight feathers during definitive prebasic molt. Therefore, maximum total primary, secondary, rectrix, and total flight feather molt scores are 90, 90, 60, and 240, respectively, in adults.

First-year (born the current calendar year) birds typically replace the outer four or five primaries, inner four to six secondaries, and all rectrices during presupplemental molt. Primary molt is most frequently initiated at P6 (see data below). Therefore, first-year birds that had replaced P6 or more distal primaries received a score of 5 for each such primary. First-year birds that had replaced P5 or more proximal primaries received a score of 0 for each such primary. Similarly, following replacement of the tertials (S7–S9), subsequent secondary molt was most frequently initiated with S5 (see data below). Therefore, first-year birds that had replaced S5 or more proximal secondaries received a score of 5 for each such secondary. Birds that had replaced S4 or more distal secondaries received a score of 0 for each such secondary. Therefore, maximum total primary, secondary, rectrix, and total flight feather molt scores are 40, 50, 60, and 150, respectively.

#### RATE AND DURATION OF FLIGHT FEATHER MOLT

The rate and duration of flight feather molt in individuals, as opposed to populations, was estimated by regression of date on total primary and total flight feather molt scores (see Pimm 1976 for statistical methodology).

#### AGE AND SEX DETERMINATION

The plumages of males and females are identical, except for some blue head plumage in some subadult males in first alternate plumage, until they begin definitive prebasic molt after their first potential breeding season at 12 to 17 months of age (Table 2). Determination of sex of these specimens was based on information provided on specimen labels. Males and females in definitive basic or definitive alternate plumage were sexed by plumage. Subadults in supplemental or first alternate plumage were distinguished in age from females in definitive basic or definitive alternate plumage by the retention of some to all juvenal (brown) remiges and greater primary coverts (Storer 1951, Fisk 1974). Similarly, first-year

TABLE 2. Sequence of molts and plumages of Painted Buntings from hatching to somatic maturity.

Age at molt	Molt-resulting plumage	Date of molt	Feathers replaced during molt	Duration of plumage	Plumage coloration
7-14 days	Born in natal down <sup>1</sup> Postnatal-juvenile	May 15-July 31	All natal plumage	1-9 days June 1-August 31	Both sexes: light drab brown Both sexes: uniformly drab brown
15-35 days	First prebasic-first basic	June 1-October 15	All body plumage except greater primary and secondary coverts	July 1-October 15	Both sexes: body plumage olive-green dorsally and yellow-green ventrally; remiges and rectrices, greater primary and secondary coverts brown
2-6 months	Presupplemental-supplemental	September 1-November 31	All body plumage except some gr. primary coverts, all rectrices, P6-P9 and S5-S9	September 15-February 15	Both sexes: all body plumage brighter olive green dorsally and yellow-green ventrally. Retained juvenal inner primaries, inner gr. primary coverts and outer secondaries are less green (more brown) than replaced inner secondaries and outer primaries
5-12 months	First prealternate-first alternate	December 15-May 15	Head and variable amount of other body plumage	February 15-September 31	Both sexes: same as supplemental plumage except males may have small patches of blue head feathers (43.4% of males, $n = 341$ ; 5.0% of females, $n = 238$ )
12-17 months	Adult prebasic-adult basic	August 1-October 15	All body and flight feathers	September 1-January 15	Females: same as female supplemental except no blue head feathers and all greater primary coverts are green. Males: head bright blue except chin and throat red; entire ventral surface, rump, and eyering red; back is bright green. Most flight feathers reddish.
17-23 months	Adult prealternate-adult alternate	January 1-May 31	Same as first prealternate molt	March 15-September 31	Both sexes: same as adult basic except females may have some blue head feathers

<sup>1</sup> Based on Parmelee (1959, 1964).

birds in juvenal or first basic plumage were distinguished from second-year (born the previous calendar year) birds in first alternate plumage by differences in plumage color (see Table 2).

#### DEFINITION OF BREEDING RANGE

During the breeding season, Painted Buntings are distributed as two disjunct eastern and western populations (Fig. 1). Unexpectedly, the breeding ranges of these two disjunct populations do not correspond to the breeding ranges of the two recognized subspecies, *ciris* and *pallidior* (American Ornithologists' Union 1957). Therefore, the disjunct eastern and western breeding populations are hereafter referred to as eastern and western Painted Buntings, respectively. Very few sight records of Painted Buntings exist for 550 km from eastern Florida (81°51'W) to western Alabama (87°42'W) (Ogden and Chapman 1967 and references cited therein). Similarly, of 1,625 specimens collected within the breeding range of *P. ciris*, only 12 (0.7%) were collected within this 550 km gap, of which none were collected west of 85°W. Subsequent discussion of breeding and wintering ranges refers to exclusive ranges, and does not include areas where breeding and wintering ranges overlap (Fig. 1). Geographic coordinates of collection localities were determined from gazetteers, atlases, and maps.

#### STATISTICAL ANALYSIS

Frequency data were analyzed in all cases using the *G*-test with Williams' correction (Sokal and Rohlf 1981:710). Total body molt score was treated as a ranked variable because it is the average of body molt scores of body areas that differ significantly in surface area and number of feathers. In comparisons of rate and timing of onset of flight feather molt, variances of pairs of regression models were tested for homoscedasticity before comparing *Y*-intercepts and slopes. The level of significance was defined as  $P < 0.05$  in all tests.

#### DESCRIPTION OF MOLTS

All descriptions of molts and plumages in Painted Buntings have been incomplete (Storer 1951, Fisk 1974) or partially incorrect (e.g., Wilson and Bonaparte 1831, Dwight 1900, Coues 1903, Sprunt 1968, Oberholser 1974). Thus, I present data concerning the timing, sequence and extent (proportion of plumage replaced) of molts, and color of the resulting plumages for each age and

sex class (summarized in Table 2), and compare these data to analogous data on Indigo Buntings (Rohwer 1986). I argue that similarities and differences in the sequence of molts and plumages between these two species indicate selection pressures which have influenced the evolution of molt strategies in these two species.

#### FIRST PREBASIC MOLT

*Sequence and extent.* This molt is exhibited only by first-year males and females and has not been distinguished by previous investigators (Dwight 1900, Storer 1951, Fisk 1974, Oberholser 1974) as a separate molt from the subsequent presupplemental molt (described below). Most or all body plumage except greater primary and greater secondary coverts is usually replaced. Incoming first basic body feathers are distinguished from incoming juvenal feathers by their brighter color (discussed below, see Table 2) and greater structural integrity (Dwight 1900). Replacement begins on the upper back, followed by the head and nape, and then the back and rump. The breast, flanks, and belly begin molting shortly after onset of molt on the dorsal side. First-year specimens were considered to be in first basic plumage if most of their juvenal plumage (except greater primary and greater secondary coverts) was replaced by first basic plumage and if they did not exhibit any molt as defined above. Of 52 first-year birds in first basic plumage, 23 retained juvenal body plumage other than greater primary and greater secondary coverts. These 23 specimens all had retained juvenal breast, belly and flank feathers, while only six had retained juvenal back or rump feathers; none had retained juvenal feathers on their head, chin or throat.

*Timing.* Parmelee (1959) collected a series of fledglings of known ages in Oklahoma (UOKLA 3407, 3409, 3410, 3412, 3414, and 3442; see acknowledgments for explanation of museum name abbreviations). These specimens indicate that this molt begins within 15 days of hatching and within one week after fledging when some juvenal body feathers and all remiges and rectrices are still sheathed and growing. This molt is completed by about 35 days after hatching. This was also the case for nestlings and fledglings examined in Austin, Texas (Thompson, unpub. data). Because Painted Buntings are often multi-brooded and fledge young as early as early June and as late as early September (e.g., Parmelee 1959), juveniles may be found in first prebasic



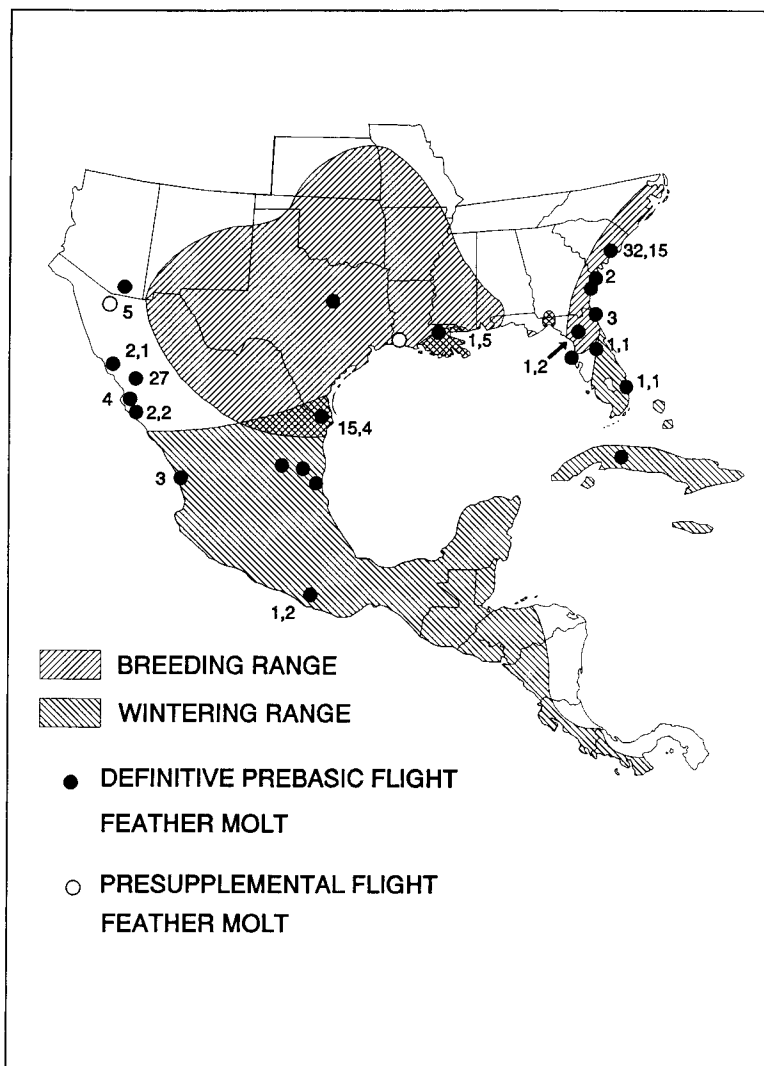


FIGURE 1. Map depicting the breeding and wintering ranges of Painted Buntings, and the locations at which first-year specimens in presupplemental flight feather molt and second-year or older specimens in definitive prebasic flight feather molt were collected. Numbers adjacent to symbols indicate number of specimens exhibiting molt. Two numbers adjacent to a symbol indicate that both first-year and second-year or older specimens were found in flight feather molt at the same locality. The first number indicates the number of second-year or older specimens, and the second number indicates the number of first-year specimens. The breeding and wintering distributions are based on 1) 776 collection localities of specimens examined in this study, 2) Bird Banding Laboratory banding summary data and recovery data, 3) records of breeding, migratory, and wintering Painted Buntings in a) Birdlore, Audubon Field Notes, and American Birds, b) The Vermillion Flycatcher (newsletter of the Tucson Audubon Society), and c) the following distributional accounts: Dearborn (1907), Carriker (1910), Howell (1911, 1928, 1932), Barbour (1923, 1943), Nice (1931), Bailey (1928), Bennett (1932), Griscom (1932), Dickey and Van Rossem (1938), Oberholser (1938, 1974), Burleigh (1944, 1958), Goodrich (1946), Sprunt (1954, 1968), Lowery (1955), Friedmann et al. (1957), Urban (1959), Ligon (1961), Smithe and Paynter (1963), Phillips et al. (1964), Slud (1964), Johnston (1965), Smithe (1966), Ogden and Chapman (1967), Sutton (1967), Monroe (1968), Taber (1968), Land (1970), Sprunt and Chamberlain (1970), Paterson (1972), Peterson and Chalif (1973), Imhof (1976), Bond (1980), Potter et al. (1980), Norris and Elder (1982), Wetmore et al. (1984), Wood and Schnell (1984), James and Neal (1986), Toups and Jackson (1987), Root (1988), Ridgely and Gwynne (1989), Stiles et al. (1989), Taylor et al. (1989), and Robinson (1990).

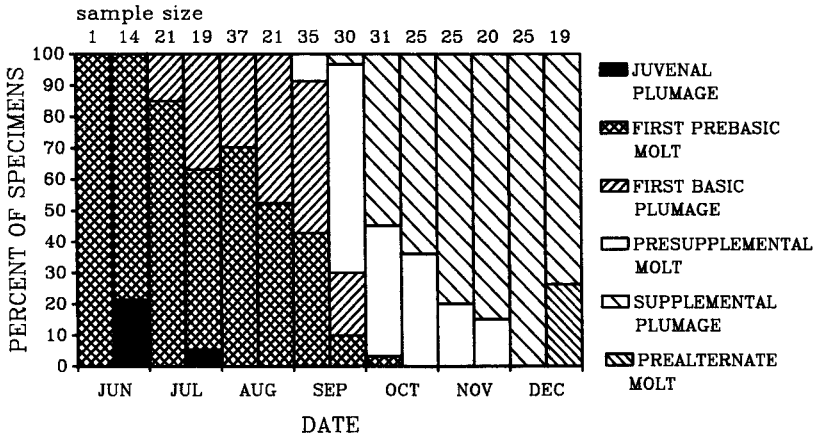


FIGURE 2. Timing of molts and plumages of first-year Painted Buntings (males and females combined).

molt from early June through mid-October (Fig. 2, Table 3).

To compare the timing of this molt between sexes, first I compared the temporal frequency distributions of first-year male and female specimens collected during the molting period from June through October. These frequency distributions did not differ significantly ( $G_{adj} = 4.399$ ,  $df = 8$ ,  $P > 0.75$ ; see Table 3) and, therefore, allowed comparison of the frequency distributions of first-year male and female specimens in molt across months of the molting period. The timing of molt did not differ significantly between the sexes ( $G_{adj} = 2.939$ ,  $df = 8$ ,  $P > 0.95$ ; Table 3).

**Location.** Most specimens (88 of 98) in first prebasic molt were collected on the breeding ground. In addition, 48 of 52 specimens in first basic plumage were collected within the breeding

TABLE 3. Temporal frequency distribution of first-year male and female Painted Buntings in first prebasic molt.

Date	Male specimens examined (n)	Male specimens in molt % (n)	Female specimens examined (n)	Female specimens in molt % (n)
June 1-15	1	100.0 (1)	0	0.0 (0)
June 16-30	10	90.0 (9)	4	50.0 (2)
July 1-15	10	100.0 (10)	7	100.0 (7)
July 16-31	10	60.0 (6)	9	77.8 (7)
Aug. 1-15	15	86.7 (13)	20	65.0 (13)
Aug. 16-31	10	50.0 (5)	8	75.0 (6)
Sept. 1-15	11	54.5 (6)	19	47.4 (9)
Sept. 16-30	14	14.3 (2)	15	66.7 (1)
Oct. 1-15	19	5.3 (1)	10	0.0 (0)

range of *P. ciris*. This indicates that most individuals complete this molt within the breeding range. However, ten of 20 first-year birds collected in exclusively migratory areas were in first prebasic molt, indicating that this molt often is completed during migration. No specimens were collected on the wintering ground in this molt. No specimen in first basic plumage (21 males, 25 females, six sex unknown) exhibited any blue or red body plumage. First basic plumage in both sexes is significantly brighter olive-green dorsally and yellow-green ventrally than is juvenal plumage. This plumage is similar to definitive female plumage, but is considerably more cryptic.

**PRESUPPLEMENTAL MOLT**

**Sequence and extent.** This molt is exhibited only by first-year males and females. All previous investigators (e.g., Dwight 1900, Storer 1951, Fisk 1974, Oberholser 1974) have mistaken this molt for first prebasic molt. All body plumage, all rectrices, and typically the outer four or five primaries and inner four to six secondaries (Table 4a) are replaced. In about 18% of males and 25% of females, one to five outer greater primary coverts also are replaced (Table 4b) at the same time as their corresponding primaries. Replacement of the four most proximal greater primary coverts was never observed (Table 4b). There was no difference between sexes in the frequency of replacing one or more greater primary coverts compared to replacing none ( $G_{adj} = 3.121$ ,  $df = 1$ ,  $P > 0.05$ ) or in the frequency distribution of their replacement ( $G_{adj} = 7.141$ ,  $df = 5$ ,  $P > 0.1$ ; see Table 4b). The sequence of body molt ap-

TABLE 4a. Site of initiation of primary and secondary molt (after S7–S9 molt) by first-year male and female Painted Buntings during presupplemental molt.

Site of initiation of primary molt	Percent of male specimens (n = 397)	Percent of female specimens (n = 283)	Site of initiation of secondary molt	Percent of male specimens (n = 361)	Percent of female specimens (n = 283)
P6	80.1	76.3	S6	39.1	44.0
P5	13.3	17.7	S5	51.5	48.7
P4	4.3	4.6	S4	9.4	7.3
P3	2.3	1.4	—	—	—

pears to follow that described previously for first prebasic molt. Primary molt is initiated most frequently at P6 (Table 4a) and proceeds in ascending order. Secondary molt begins with S7–S9, which do not appear to be replaced in any particular order, and is subsequently followed by S4, S5, and/or S6 in ascending order. Rectrices were molted simultaneously in most cases (13 of 14), as indicated by their similar length during replacement, and rarely in ascending order (1 of 14). First-year birds were considered to be in presupplemental molt if they either exhibited symmetric flight feather molt or exhibited body molt and had replaced their greater secondary coverts.

No specimens ( $n = 159$  males, 137 females) in supplemental plumage exhibited any blue feathers; red feathers were found in 11 (7%) males and one (<1%) female. Supplemental plumage is somewhat brighter olive-green dorsally and considerably brighter yellow-green ventrally than first basic plumage. Birds in this plumage can be distinguished from adult females by their retained juvenal inner primaries, inner greater primary coverts, and outer secondaries. Retained juvenal remiges and greater primary coverts become considerably more similar in color (more

TABLE 4b. Frequency of replacement of juvenal (brown) with green outer greater primary coverts by first-year male and female Painted Buntings during presupplemental molt.

Greater primary coverts replaced	Percent of male specimens (n = 428)	Percent of female specimens (n = 324)
0	82.5	75.0
1	3.7	6.5
2	5.6	5.9
3	6.1	11.7
4	1.9	0.6
5	0.2	0.3

TABLE 5. Temporal frequency distribution of first-year male and female Painted Buntings in presupplemental body and/or flight feather molt.

Date	Male specimens examined (n)	Male specimens in molt % (n)	Female specimens examined (n)	Female specimens in molt % (n)
Sept. 1–15	11	63.6 (7)	19	47.4 (9)
Sept. 16–30	14	78.6 (11)	15	73.3 (11)
Oct 1–15	19	36.8 (7)	10	70.0 (7)
Oct. 16–31	12	33.3 (4)	12	41.7 (5)
Nov. 1–15	12	33.3 (4)	12	91.7 (11)
Nov. 16–30	9	22.2 (2)	11	9.1 (1)

green and less brown) to supplemental remiges and greater primary coverts as they wear. Supplemental remiges are not sufficiently longer than the juvenal remiges they replace to allow discrimination of subadult males and females from adult females based on remex length. In addition, retained remiges become more green due to wear than do retained upper greater primary coverts. Thus, retained greater primary coverts are the best criterion for distinguishing males and females in supplemental or first alternate plumage from females in definitive alternate or definitive basic plumage.

*Timing.* Presupplemental body and flight feather molt typically occurs from early September through late October. However, a few specimens exhibited a small amount of body molt until late November (Fig. 2, Table 5).

Regression of date on primary molt score indicates no significant relationship between these variables for males ( $n = 20$ ) (one-tailed  $t$ -test,  $t = 0.0908$ ,  $df = 18$ ,  $P > 0.45$ ), females ( $n = 19$ ,  $df = 17$ ,  $P > 0.2$ ), or both sexes combined ( $t = 0.4379$ ,  $df = 35$ ,  $P > 0.25$ ). However, regression of date on total flight feather molt score (TFFMS) does indicate a significant relationship ( $t = 2.5017$ ,  $df = 36$ ,  $P < 0.01$ ). Comparison of Y-intercepts (at  $X = 86$ , the minimum TFFMS in the data set; see Fig. 3) and slopes of regressions for males versus females indicates no significant difference in the date of onset ( $t = 0.8702$ ,  $df = 37$ ,  $P > 0.2$ ) or rate ( $t = 0.3499$ ,  $df = 36$ ,  $P > 0.5$ ) of molt. The average duration of molt is 47 days.

*Location.* The location of presupplemental flight feather molt differs dramatically between eastern and western Painted Buntings. No specimens were collected on the wintering range in first basic plumage. This indicates that most, if not all, Painted Buntings must initiate this molt

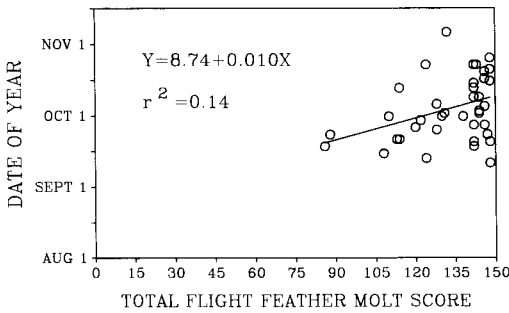


FIGURE 3. Regression of collection date against total flight feather molt score during presupplemental molt for subadults (males and females combined). In the regression model, Y is expressed as a decimal form of month, e.g., for the date 15 October,  $Y = 10.50$ .

before reaching the wintering ground. Seventeen (89%) eastern specimens in this molt were collected on the breeding ground (Fig. 1), indicating that eastern Painted Buntings usually begin this molt on the breeding ground. The remaining two (11%) eastern specimens in molt were collected on the wintering ground (Fig. 1), but probably initiated this molt on the breeding ground. In addition, seven eastern specimens were collected from within their breeding range in supplemental plumage, indicating that eastern Painted Buntings often complete this molt on the breeding ground.

In contrast to eastern Painted Buntings, only one (5%) western Painted Bunting was collected on the breeding ground in this molt, and this specimen was collected very close to a wintering area along the Gulf of Mexico (Fig. 1). Further, no western specimens were collected from their breeding range in supplemental plumage. These results indicate that western Painted Buntings rarely begin, much less complete, presupplemental molt on their breeding ground. An additional eight (40%) specimens in molt were collected in exclusively migratory areas of southeastern Arizona, Sonora, and northern Sinaloa, indicating that nearly half of all western Painted Buntings undergo at least part of this molt in exclusively migratory areas. In addition, western specimens were collected in these migratory areas in first basic plumage ( $n = 4$ ) and presupplemental body molt ( $n = 6$ ), prior to beginning flight feather molt. This shows that many western Painted Buntings do not begin this flight feather molt until they reach these migratory areas. Of the remaining specimens in this molt, nine (45%)

were collected in areas of overlap between breeding and wintering ranges (discussed further in discussion), and only two (10%) were collected on the wintering ground, probably having initiated molt in migratory areas as discussed above. This indicates that most, if not all, western Painted Buntings that undergo this molt in migratory areas do not continue their migration to the wintering ground until their flight feather molt is complete.

#### PREALTERNATE MOLT

*Sequence and extent.* After completing this study, I found that this molt had been recognized previously by Fisk (1974) who stated that "both first-year [second-year] and adult birds had a partial spring molt, replacing the abdominal, at least some breast feathers, and at least some feathers in the orbital region, lores, and chin. This molt is rapid, the short facial and chin quills exploding in a day or two." Fisk also recognized that subadult males grow female-like feathers during this molt when she stated that "the fresh straw yellow abdominal feathers of the immature [subadult male or female] bird, or the adult female, are partially grown one day and fully grown two days later. . . . An immature male may acquire a scattering of blue feathers in the head at this time, but . . . the ventral parts remain yellow." Others (e.g., Storer 1951) have noted that subadult males may have some blue head plumage in spring but not in winter, but have attributed this change to wear or adventitious molt rather than a prealternate molt. In addition, it is quite surprising that, subsequent to Fisk (1974), all investigators of delayed plumage maturation overlooked Fisk's discovery of prealternate molt in Painted Buntings, and the growth of female-like feathers by subadult males during this molt.

My data completely corroborate Fisk's results that this molt occurs in all age and sex classes. Except blue and, rarely, red plumage in some subadults and adult females (Table 2, Fig. 4), all alternate plumage in all age and sex classes is identical in color to the plumage that preceded it. The alternate plumages of adult females and subadult males and females are essentially identical (except for some or all greater primary coverts) being bright olive-green dorsally and yellow-green ventrally. However, a greater proportion of subadult males exhibit limited blue head plumage than either subadult females ( $G_{\text{adj}} = 33.492$ ,  $df = 1$ ,  $P < 0.001$ ) or adult females

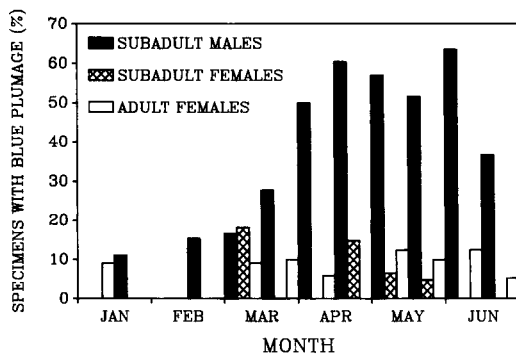


FIGURE 4. Percentage of Painted Buntings with any blue plumage by age-sex class, excluding adult males, from January through June.

( $G_{adj} = 30.405$ ,  $df = 1$ ,  $P < 0.001$ ; Fig. 4). Incoming alternate head plumage of subadult males was green in 14 specimens (AMNH 60063, 785749, 365308; DMNH 48703, 48707; FMNH 22930; LSU: 49448, 17629; MCZ 310689, 261372; MLOCAL 49405, 26451; UMINN 29875, 29869), blue and green in three specimens (FMNH 22932; LSU 99884; MLOCAL 25945), and only blue in one specimen (MCZ 261371).

Total body molt score (TBM) was used to evaluate molt intensity among age and sex classes (Fig. 5). Molt intensity was significantly higher in adult males than females ( $n = 697$ , Mann-Whitney  $U$  test,  $U = 35,677$ ,  $P = 0.021$ ), but did not differ between subadult males and females ( $n = 224$ ,  $U = 6,350$ ,  $P = 0.557$ ). In addition, molt intensity was significantly higher in adult males than subadult males and females ( $n = 786$ ,  $U = 59,216$ ,  $P = 0.007$ ), but did not differ between adult females and subadult males and females ( $n = 359$ ,  $U = 15,111$ ,  $P = 0.998$ ).

It is not possible to distinguish between completely grown (unsheathed) alternate body feathers and feathers of the preceding plumage of the same color. Therefore, on museum specimens, it also is not possible to determine either the average extent of this molt among age and sex classes or the proportion of molt completed in individuals. However, it is probable that examination of museum skins underestimates the proportion of birds molting feathers on parts of the body other than the head.

*Collection of molt data from live versus museum specimens.* Based on my examination of museum skins, molt appears to be limited to the head in most cases (85 of 92 specimens). Molt

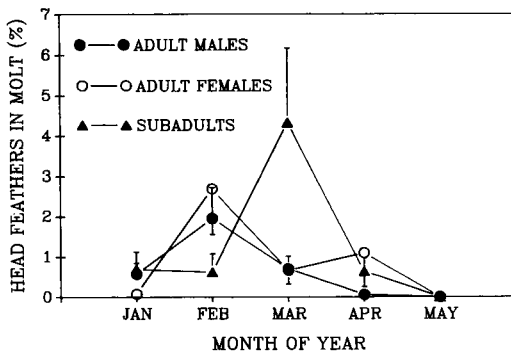


FIGURE 5. Percentage of head plumage in molt during prealternate molt in Painted Buntings by age and sex class. Values represent means  $\pm$  1 SE.

on areas of the body other than the head was observed in only two subadult males, one subadult female, three adult females, and one adult male. However, examination of museum skins underestimates the proportion of birds molting feathers on parts of the body other than the head because molting feathers are more difficult to see on the body than on the head of museum skins as compared to live birds. This is illustrated by four lines of evidence.

First, museum skin labels often indicated presence of prealternate body molt that I could not find, e.g., the label of an adult male (LSU 113340) stated "moderate overall body molt," but I could not find any.

Second, many areas on the body of museum skins can not be examined because they are covered by the wings and legs of the specimens.

Third, among specimens of Painted Buntings in prealternate molt, Fisk (unpub. data) found molting ventral and dorsal feathers in a much higher proportion of live specimens (15 of 61) than I did in museum skins (7 of 87) ( $G$ -test,  $G_{adj} = 3.931$ ,  $df = 1$ ,  $P < 0.05$ ). This is a valid comparison for the following reasons. First, there is no significant difference among the frequency distributions of subadult and adult male and female specimens examined in this study for the period from December through May ( $G_{adj} = 1.007$ ,  $df = 15$ ,  $P > 0.995$ ; Tables 6a, b) or in Fisk's study for the period from January through April ( $G_{adj} = 1.470$ ,  $df = 6$ ,  $P > 0.95$ ; Table 7). This indicates that no age or sex class is disproportionately represented in the data in any month within either study. Second, the proportion of specimens in molt does not differ among age and

TABLE 6a. Temporal frequency distribution of first prealternate molt observed in museum specimens of subadult male and female Painted Buntings.

Month	Males examined (n)	Males in head molt % (n)	Males in body <sup>1</sup> molt % (n)	Females examined (n)	Females in head molt % (n)	Females in body <sup>1</sup> molt % (n)
Dec.	17	17.6 (3)	0.0 (0)	23	8.7 (2)	0.0 (0)
Jan.	14	0.0 (0)	0.0 (0)	35	8.6 (3)	0.0 (0)
Feb.	26	11.5 (3)	0.0 (0)	32	3.1 (1)	0.0 (0)
Mar.	36	19.4 (7)	2.8 (1)	32	21.9 (7)	3.1 (1)
Apr.	63	9.5 (6)	0.0 (0)	38	0.0 (0)	0.0 (0)
May	129	0 (0)	0.8 (1)	67	0.0 (0)	0.0 (0)

<sup>1</sup> These specimens may also exhibit head molt.

sex classes in this study during the period from December through May ( $G_{adj} = 3.436$ ,  $df = 3$ ,  $P > 0.25$ ; Tables 6a, b) or in Fisk's study from January through April ( $G_{adj} = 1.805$ ,  $df = 2$ ,  $P > 0.25$ ; Table 7). This indicates that the frequency of molt does not differ significantly among age and sex classes and, therefore, allows age and sex classes to be combined for further analysis. Third, there is no significant difference between Fisk's study (unpub. data) and this study in the frequency distribution of specimens (age and sex classes combined) from January through April ( $G_{adj} = 6.596$ ,  $df = 3$ ,  $P > 0.05$ ; Tables 6a and 6b combined versus Table 7).

Fourth, growing "pin" feathers are often lost from specimens during specimen preparation.

Fisk usually observed only a small number of growing feathers in individual birds at any one time during this molt, although she estimated individuals rarely had as much as 80% of their body feathers in molt. In addition, Fisk's data indicate that molt occurs in subadults and adults in most, if not all, feather tracts of the head and body including greater and lesser tail coverts and median and lesser wing coverts, and that molt is extensive in at least some individuals. This sug-

gests that this molt is more extensive in all age and sex classes than is indicated by my analysis of museum specimens.

*Timing.* First prealternate molt begins in mid-December, only shortly after completion of pre-supplemental molt in late November, and is completed by mid-May (Fig. 5, Tables 6a and 7). Timing of this molt is also reflected by the development of blue head plumage in subadults (Fig. 4). Similarly, definitive prealternate molt occurs from early January through late May (Fig. 5, Tables 6b and 7). At the population level, presupplemental and definitive prebasic molts nearly overlap in time and first and definitive prealternate molts in subadults and adults, respectively.

That prealternate molt in subadults and adults is a functionally separate event from the fall molt that preceded it, and not a continuation of it, is strongly suggested by three points. First, in all age and sex classes, the percentage of birds in prealternate molt increases from late December through February and March, and decreases through April and May (Tables 6a, b and 7). Second, specimens in presupplemental and definitive prebasic molt complete head molt usu-

TABLE 6b. Temporal frequency distribution of definitive prealternate molt observed in museum specimens of adult male and female Painted Buntings.

Month	Males examined (n)	Males in head molt % (n)	Males in body <sup>1</sup> molt % (n)	Females examined (n)	Females in head molt % (n)	Females in body <sup>1</sup> molt % (n)
Dec.	50	0.0 (0)	0.0 (0)	22	0.0 (0)	0.0 (0)
Jan.	84	8.3 (7)	0.0 (0)	25	4.0 (1)	4.0 (1)
Feb.	88	18.2 (16)	0.0 (0)	29	20.7 (6)	3.4 (1)
Mar.	103	13.6 (14)	0.0 (0)	21	19.0 (4)	0.0 (0)
Apr.	287	0.0 (0)	0.3 (1)	60	5.0 (3)	3.3 (2)
May	307	0.3 (1)	0.0 (0)	74	0.0 (0)	0.0 (0)

<sup>1</sup> These specimens may also exhibit head molt.

TABLE 7. Temporal frequency distribution of prealternate molt observed in adult male and female live specimens of Painted Buntings (Fisk, unpublished data).

Month	SY ♂♂ + ♀♀ examined (n)	SY ♂♂ + ♀♀ in head molt % (n)	SY ♂♂ + ♀♀ in body <sup>1</sup> molt % (n)	ASY ♂♂ examined (n)	ASY ♂♂ in head molt % (n)	ASY ♂♂ in body <sup>1</sup> molt % (n)	ASY ♀♀ examined (n)	ASY ♀♀ in head molt % (n)	ASY ♀♀ in body <sup>1</sup> molt % (n)
Jan.	20	0.0 (0)	0.0 (0)	12	0.0 (0)	0.0 (0)	5	0.0 (0)	0.0 (0)
Feb.	31	19.3 (6)	0.0 (0)	18	44.4 (8)	0.0 (0)	15	46.7 (7)	0.0 (0)
Mar.	42	14.3 (6)	14.3 (6)	26	19.2 (5)	3.8 (1)	18	27.8 (5)	0.0 (0)
Apr.	54	3.7 (2)	7.4 (4)	36	11.1 (4)	0.0 (0)	31	9.7 (3)	12.9 (4)

<sup>1</sup> These specimens may also exhibit head molt.

ally by late September and always by mid-October. Third, adult females and subadult males and females frequently grow some blue and red feathers during this molt (Fig. 4), but such feathers are never grown during presupplemental or definitive prebasic molt.

To compare the timing of this molt among age and sex classes, first I compared the frequency distributions of male and female specimens within age classes from December through May. These distributions differed significantly between subadult males and subadult females ( $G_{adj} = 15.481$ ,  $df = 5$ ,  $P < 0.01$ ; see Table 6a), but not between adult males and adult females ( $G_{adj} = 4.602$ ,  $df = 5$ ,  $P > 0.25$ ; see Table 6b). Therefore, comparison of the timing of this molt in males and females was done by comparing frequencies of 1) subadult males and subadult females in molt during each month of the molting period, and 2) adult males and adult females in molt across all months of the molting period. No significant differences in the frequency of molt were found between subadult males and subadult females in any month ( $G_{adj} \leq 1.293$ ,  $df = 1$ ,  $P > 0.25$ ), or between adult males and adult females from December through May ( $G_{adj} = 3.618$ ,  $df = 5$ ,  $P > 0.5$ ). This indicates that the timing of this molt does not differ significantly between sexes within age classes. Therefore, frequencies of male and female specimens were combined within age classes in each month for further analysis. To compare the timing of this molt between age classes, I compared the frequency distributions from December through May of subadult and adult specimens. These distributions differed significantly between age classes ( $G_{adj} = 11.385$ ,  $df = 5$ ,  $P < 0.05$ ). Therefore, comparison of the timing of this molt in subadults versus adults was done by comparing frequencies of subadults

versus adults in molt during each month of the molting period. No significant difference in the frequency of molt between age classes was detected in any month ( $G_{adj} \leq 3.434$ ,  $df = 1$ ,  $P > 0.05$ ; see Tables 6a, b), indicating that the timing of this molt does not differ significantly between age classes.

An identical analysis of Fisk's data (unpub.) yielded similar results. The frequency distributions of male and female specimens within age classes from January through April did not differ significantly between adult males and females ( $G_{adj} = 0.909$ ,  $df = 3$ ,  $P > 0.75$ ; see Table 7). Fisk did not sex subadults in her study because it is not possible to do so except by laparotomy or observing sex-specific behaviors. Therefore, the frequency distributions of subadult males and females could not be compared. Adult males and females did not differ significantly in the timing of this molt ( $G_{adj} = 0.453$ ,  $df = 3$ ,  $P > 0.9$ ; see Table 7). In addition, the frequency distributions of subadult and adult specimens did not differ significantly ( $G_{adj} = 0.563$ ,  $df = 3$ ,  $P > 0.9$ ), and no significant difference in the timing of molt between age classes was detected ( $G_{adj} = 1.400$ ,  $df = 3$ ,  $P > 0.25$ ; see Table 7).

*Location.* Ninety specimens in first and definitive prealternate molt were collected on the wintering ground as compared to only two on the breeding ground. This indicates that this molt is usually completed on the wintering ground, but rarely is continued on the breeding ground. This is further supported by the 1) absence of prealternate molt in live specimens (adults: 19 males, 8 females; subadults: 13 males, 9 females) mist-netted on the breeding ground in Austin, Texas during May, 1984, and 2) lack of change in plumage color in subadult males captured in April or May and recaptured later in the breeding season

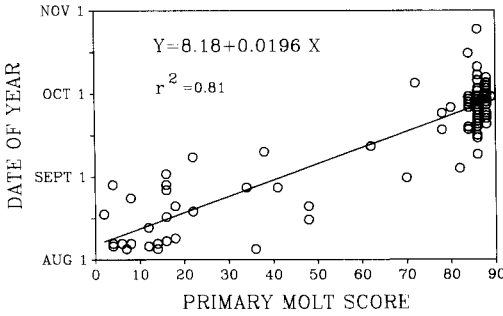


FIGURE 6. Regression of collection date against primary molt score during definitive prebasic molt in Painted Buntings for adult males and females (combined). In the regression model, Y is expressed as a decimal form of month, e.g., for the date 15 October, Y = 10.50.

at the same locality in Austin, Texas ( $n = 17$ ) and in coastal South Carolina (T. A. Beckett III, pers. comm.).

**DEFINITIVE PREBASIC MOLT**

*Sequence and extent.* This is a complete and very intense molt exhibited by second-year and older males and females. The intensity of this molt renders molting birds nearly flightless during the intermediate stages of this molt, thereby causing them to become very secretive at this time (Thompson, unpub. data; T. A. Beckett III, pers. comm.). This is also illustrated by the relative lack of adult specimens in intermediate stages of molt (Fig. 6). Body molt begins on the upper back and progresses in the following overlapping se-

quence: all primary and secondary coverts, head (including chin, throat, and nape) and lower back, and underside. Flight feather molt typically begins with P1, followed shortly thereafter by the secondaries and rectrices. All primaries and S1-S6 molt in ascending order. S7-S9 molt first, followed by S1-S6. Rectrices appear to be replaced synchronously in most cases (21 of 28 specimens), and in ascending order in the rest ( $n = 7$ ).

Contrary to many earlier sources (e.g., Dwight 1900, Sprunt 1968, Oberholser 1974), the presence of female-like olive-green body or flight feathers in adult males is not an indication of an incomplete prebasic molt by subadult males, but rather indicates adventitious feather loss and replacement, i.e., replacement of feathers lost and replaced at a time other than the normal molting period (Storer 1951, Fisk 1974). S7-S9 and P1-P3 (occasionally 4 and 5) of adult males are usually partly or totally bright green, being similar in color to their bright green dorsal body plumage, and thus are easily distinguished from adventitiously replaced olive-green flight feathers.

*Timing.* Adult prebasic molt typically occurs from early August through early October (Fig. 7), but some specimens exhibited body molt until mid-November. Linear regression of date on primary molt score indicates that duration of flight feather molt is approximately 54 days (Fig. 6). Comparison of Y-intercepts and slopes of regressions of date on primary molt score for males and females indicates that flight feather molt does

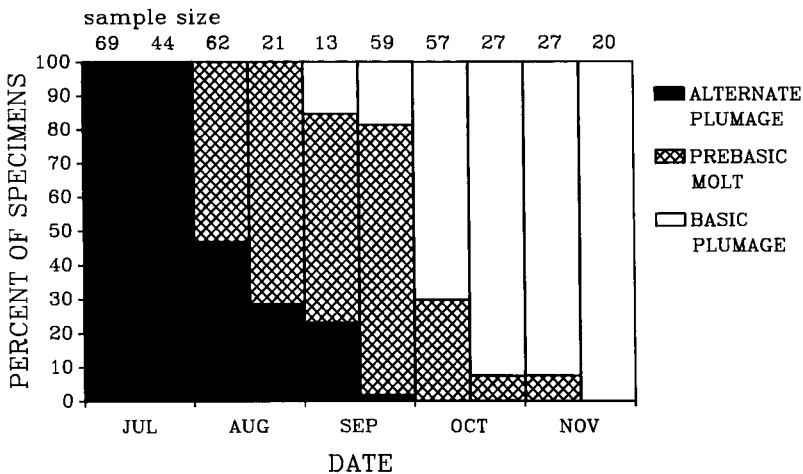


FIGURE 7. Timing of molts and plumages of second-year and older male and female Painted Buntings from July through November.



not differ between the sexes in its rate ( $t$ -test,  $t = 0.8998$ ,  $df = 93$ ,  $P > 0.2$ ) or date of onset ( $t = 1.621$ ,  $df = 94$ ,  $P > 0.1$ ).

*Location.* Like presupplemental flight feather molt, the location of definitive prebasic flight feather molt differs dramatically between eastern and western Painted Buntings. No specimens were collected on the wintering range in first or definitive alternate plumage. This indicates that most, if not all, Painted Buntings must initiate this molt before reaching the wintering ground. Forty (93%) eastern specimens in this molt were collected on the breeding ground (Fig. 1), indicating that eastern Painted Buntings usually begin this molt on the breeding ground. The remaining three (7%) eastern specimens in molt were collected on the wintering ground (Fig. 1), but probably initiated this molt on the breeding ground. This conclusion is corroborated by Fisk (1974, unpub. data, pers. comm.) who studied Painted Buntings on the wintering ground in southern Florida. She never captured any adults in first or definitive alternate plumage prior to definitive prebasic molt, but did capture 11 adults "in [adult prebasic] molt between 25 September and 27 October." In addition, 13 eastern specimens were collected from within their breeding range in definitive basic plumage, indicating that eastern Painted Buntings often complete this molt on the breeding ground. This conclusion is corroborated by Tipton and Tipton (1978) who banded two second-year males in first alternate plumage in South Carolina on 21 and 23 July 1977. Both birds were recaptured at the same locality on 21 September 1977, both having completed definitive prebasic molt "except for waxy sheaths on primaries eight and nine."

In contrast to eastern Painted Buntings, within the breeding range of western Painted Buntings, only one (1.7%) western Painted Bunting was collected in this molt (Fig. 1), and only one specimen was collected in definitive basic plumage. These results indicate that western Painted Buntings rarely begin, much less complete, this molt on their breeding ground. An additional 36 (60%) specimens in molt were collected in exclusively migratory areas of southeastern Arizona, Sonora, and northern Sinaloa, indicating that most western Painted Buntings undergo at least part of this molt in exclusively migratory areas. In addition, western specimens were collected in these migratory areas in first and definitive alternate plumage ( $n = 9$ ) and definitive prebasic body molt ( $n$

$= 10$ ), prior to beginning flight feather molt. This shows that many western Painted Buntings do not begin this flight feather molt until they reach these migratory areas. In addition, three specimens were collected in migratory areas in fresh definitive basic plumage, indicating that at least some individuals complete molt before continuing their migration to the wintering ground. Of the remaining specimens in flight feather molt, 16 (26.7%) were collected in areas of overlap between breeding and wintering ranges (discussed further in discussion), and only seven (11.7%) were collected on the wintering ground, probably having initiated molt in migratory areas as discussed above. This further suggests that most, if not all, western Painted Buntings that undergo this molt in migratory areas do not continue their migration to the wintering ground until their flight feather molt is complete.

#### COMPARISON OF MOLTS AND PLUMAGES BETWEEN INDIGO AND PAINTED BUNTINGS

This comparison indicates that Painted and Indigo Buntings exhibit very similar seasonal timing and extent of all molts in all age and sex classes. However, most molts and plumages differ dramatically between Painted and Indigo Buntings in two ways: 1) whether molt occurs on the wintering, migratory, or breeding ground, and 2) the seasonal change in male plumage color and conspicuousness resulting from molt.

#### FIRST PREBASIC MOLT

Juvenile male and female Painted Buntings begin first prebasic molt of most to all body feathers (except primary and secondary coverts) within a week of fledging that results in a first basic plumage that is brighter green dorsally and yellow ventrally. In both males and females, first basic plumage is more similar to definitive female plumage than is the previous juvenal plumage. In Indigo Buntings, the age of onset and seasonal timing of this molt is very similar to that of Painted Buntings, and first basic plumage in both males and females is also more similar to female definitive basic plumage than is the previous juvenal plumage (Rohwer 1986). The existence of this molt raises an obvious question. Why do fledgling Painted and Indigo Buntings undergo this nearly complete body molt that does not result in a substantial change in plumage color and subsequently undergo a second complete molt

only one to three months later? Juvenal plumage in both species is more compressible and has less structural integrity (less interlocking barbules and lower density of barbs on feathers) than subsequent plumages (Thompson, unpub. data). Thus, juvenal plumage probably facilitates heat transfer during brooding, but is poorly adapted to protecting juveniles from adverse abiotic factors such as wind, rain, incident solar radiation, and physical abrasion. Selection may have favored evolution of juvenal plumage that facilitates heat transfer from the brooding female to young in the nest, and replacement of this plumage as soon as possible after fledging with a structurally stronger plumage that offers more protection from the physical environment (Webb et al. 1990).

#### PRESUPPLEMENTAL MOLT

Within three months after completing first prebasic molt, and usually before arrival on the wintering ground, first-year male and female Painted Buntings subsequently undergo a presupplemental molt of all body plumage, all rectrices, the inner four to six secondaries, and the outer four or five primaries. The resulting supplemental plumage is significantly brighter green dorsally and yellow ventrally than first basic plumage, and is essentially identical in color to definitive female plumage. The extent and seasonal timing of this molt is very similar in Indigo Buntings. However, this molt differs between Painted and Indigo Buntings in two striking ways. First, about 90% of Painted Buntings complete this molt before arrival on the wintering ground whereas at least 90% of Indigo Buntings do not begin this molt until they reach the wintering ground (Rohwer 1986). Second, supplemental plumage resulting from this molt is essentially identical to female definitive basic plumage in subadult male Painted Buntings, but is essentially identical to male definitive basic plumage in subadult male Indigo Buntings (Rohwer 1986).

#### PREALTERNATE MOLT

In Painted Buntings, this molt 1) occurs almost exclusively on the wintering ground, 2) results in growth of adult female-like plumage by subadult males, and 3) is similar in extent among age and sex classes. In contrast, in Indigo Buntings this molt 1) is continued on the breeding ground in about 17% of specimens, 2) results in growth of exclusively adult male-like plumage by subadult males, and 3) is less extensive in subadults than

adults which typically replace S7–S9 (Rohwer 1986). Adult males and females of both species grow adult male- and female-like plumage, respectively, during this molt.

Wingfield (pers. comm.) concluded from a review of the literature that physiological control of plumage color typically is independent of sex steroids in species such as Painted Buntings that do not change plumage color seasonally after reproductive maturity, but is dependent on sex steroids in species such as Indigo Buntings that do change plumage color seasonally after reproductive maturity. Testis size of subadult male Painted Buntings does not differ significantly from that of adult males from March through June (Thompson, unpub. data), and gonadal hypertrophy is significantly advanced in both subadults and adults by April. This suggests that circulating plasma sex steroid (testosterone) levels are elevated in subadult male Painted Buntings when they grow green (female-like) feathers during first prealternate molt, and, therefore, supports Wingfield's conclusion that physiological control of plumage color typically is independent of sex steroids in species that do not change plumage color seasonally after reproductive maturity.

However, Lowery (1955:58) states that "the brilliant livery of the male Painted Bunting is brought on by secretions of the mature male gonads which do not become activated until the spring following birth. Before this the male is attired like the female. Experimentally, in the laboratory, adult males can be made to assume the color of the female by injection of female hormones. Conversely, the female can be made to take on the male attire by injection of male hormones." Unfortunately, Lowery (1955) gives no additional details or citations regarding these experiments. A comparison of circulating plasma sex steroid levels between subadult and adult males in Painted and Indigo Buntings would be a valuable contribution to our knowledge of the hormonal control of plumage color.

#### ADULT PREBASIC MOLT

Most Painted and Indigo Buntings complete this molt before arrival on the wintering ground. This molt does not cause any seasonal change in plumage color in adult females of either species. In males, however, this molt replaces conspicuous breeding plumage with an identical conspicuous winter plumage in Painted Buntings,

but with a much more cryptic and female-like winter plumage in Indigo Buntings.

This comparison of the molts and plumages of Painted and Indigo Buntings illustrates that both species exhibit the same sequence of molts during similar months of the year, but that the location (breeding, migratory, or wintering area) of molt and the seasonal changes in plumage color and conspicuousness differ dramatically. Lazuli Buntings, *Passerina amoena*, exhibit the same set of similarities and differences in their sequence of molts and plumages (Young, in press), thus further corroborating this conclusion. Although no strong conclusions can be inferred from these comparisons, the apparent pattern of similarities and differences among these three species of *Passerina* suggests that the extent, timing with respect to breeding and migration, and location of molt, as well as the seasonal color change caused by molt, are less phylogenetically constrained than are the sequence and calendar timing of molt.

#### IMPLICATIONS FOR MOLT-MIGRATION IN PASSERINES

In most birds, flight feather molt typically occurs on the breeding ground prior to migration or, more rarely, on the wintering ground after migration. Alternatively, flight feather molt may begin on the breeding ground, be suspended during migration, and be completed on the wintering ground. Molt of flight feathers during migration, called molt-migration, is rare. It has been documented previously in many species of waterfowl (Herter et al. 1989 and refs. cited therein), and raptors (Thiollay 1978), and in some shorebirds, grebes, flamingos, cranes, and auk (Jehl 1990), but in no other nonpasserines and only five species of passerines: Western Kingbirds, *Tyrannus verticalis* (Phillips et al. 1964), Swainson's Thrushes, *Catharus ustulatus* (Cherry 1985), Northern Orioles (Rohwer and Manning 1990), Lazuli Buntings (Young, in press), and Yellow-breasted Buntings, *Emberiza aureola* (Stresemann and Stresemann 1966, cited in Young, in press). The occurrence of molt-migration in western Painted Buntings was previously recognized by Phillips et al. (1964) who stated that, prior to "prebasic" [presupplemental or definitive prebasic] molt, Painted Buntings migrate from more easterly breeding areas to southeastern Arizona and northern Sonora where they begin and complete "prebasic" [presupplemental

or definitive prebasic] molt before continuing on to the wintering ground. This study documents molt-migration by first-year and adult Painted Buntings, and illustrates that the pattern of molt-migration in this species is very similar to that exhibited by Northern Orioles and Lazuli Buntings.

Northern Orioles are classified into two geographically contiguous subspecies: Baltimore Orioles (*I. g. galbula*) and Bullock's Orioles (*I. g. bullockii*) which breed extensively throughout southern Canada and most of the continental United States east and west of central Texas, respectively. Lazuli Buntings have an extensive breeding range in the midwestern and western United States. Drought conditions often prevail in the midwestern and western United States in late summer and fall. At this time, Lazuli Buntings (Young, in press) and Bullock's Orioles (Rohwer and Manning 1990) usually migrate to and undergo a complete molt in desert areas of the southwestern United States and northwestern Mexico that are outside their breeding and wintering ranges. Conversely, Baltimore Orioles usually complete this molt prior to fall migration. Rohwer and Manning (1990) and Young (in press) argue that these desert locations exhibit a large increase in plant and insect life in response to "monsoon" rains that occur predictably in these areas in late summer and fall. In turn, they argue that selection has favored evolution of molt-migration strategies in Bullock's Orioles and Lazuli Buntings as a mechanism to allow these species to molt in an area with greater food resources than exist at the same time of year on their breeding or wintering ground. In addition, most Baltimore Orioles, but not Bullock's Orioles, probably migrate across the Gulf of Mexico en route to their wintering ground in Central and South America. Rohwer and Manning (1990) argue that, as a consequence, selection has favored Baltimore Orioles, but not Bullock's Orioles, to maximize their flight efficiency during fall migration by completing flight feather molt prior to fall migration.

Except in coastal areas, western Painted Buntings inhabit areas that often experience drought and food shortage in late summer and fall. Conversely, eastern Painted Buntings inhabit coastal areas that rarely experience drought and food shortage in late summer and fall. In addition, like Northern Orioles, most eastern and western Painted Buntings migrate across and around the

Gulf of Mexico, respectively, to their wintering ground in Central America (Storer 1951, Bird Banding Lab, unpub. data). Figure 1 illustrates that presupplemental and definitive prebasic flight feather molt occurs on the breeding ground in the eastern population in about 90% of cases, but in the western population in less than 5% of cases. About 50% of the western population undergo flight feather molt in exclusively migratory areas of southeastern Arizona, Sonora, and northern Sinaloa. An additional 20–25% of western specimens in flight feather molt were collected in the Rio Grande Valley of Texas where the breeding and wintering ranges of Painted Buntings overlap. This area, like the desert southwest, experiences similar “monsoon” conditions in late summer that cause large increases in seeds and insects. Thus, this area probably serves as an alternate staging ground for flight feather molt. Only about 10% of specimens from the eastern and western populations were found in flight feather molt on the wintering ground. The similarities in the patterns of molt-migration among Painted Buntings, Lazuli Buntings, and Northern Orioles suggests that these patterns evolved in response to similar selection pressures in these species.

#### IMPLICATIONS FOR THEORIES OF DELAYED PLUMAGE MATURATION

The implications of seasonal changes in plumage color in subadult male Painted Buntings for winter and summer hypotheses are summarized in Table 1 and explained below.

#### WINTER HYPOTHESES

All three winter hypotheses predict that plumage of subadult males should be less conspicuous than that of adult males in winter and assume that the benefits of such plumage in winter outweigh the costs of such plumage in summer.

The *winter status signaling hypothesis* (Rohwer 1975, 1978a, 1982, 1985; Rohwer and Butcher 1988) predicts that winter plumage of subadult males should reliably indicate their fighting ability. Subadult male Painted Buntings must compete with adult males and females in winter. Painted Buntings are often multi-brood and fledge young as early as early June (e.g., LSU 13989) and as late as early September (e.g., Parmelee 1959, Sutton 1967). As a result, during their first fall and winter, subadult males vary greatly in relative age and, therefore, presumably in fight-

ing ability as well. Thus, the winter status signaling hypothesis predicts that the extent of adult male-like winter plumage acquired by subadult males as a result of presupplemental molt should be correlated with fighting ability and, thus, should vary considerably among subadult males. In addition, the more conspicuous that subadult male winter plumage is, on average, relative to the preceding fall plumage, the stronger is the support for the winter status signaling hypothesis.

Within three months after completing first prebasic molt, and usually before arrival on the wintering ground, first-year male and female Painted Buntings undergo a presupplemental molt of all body feathers and many flight feathers. The resulting supplemental plumage in all subadult males is essentially identical in color to definitive female plumage, and is similar to but more conspicuous than the previous first basic plumage. This is inconsistent with the winter status signaling hypothesis.

The *winter cryptic hypothesis* (Ewald and Rohwer 1980, Rohwer et al. 1983, Rohwer 1986, Rohwer and Butcher 1988) predicts that subadult male winter plumage should be equally or more cryptic than the preceding fall plumage. Supplemental plumage is significantly more conspicuous than the first prebasic plumage that preceded it. Thus, the data are inconsistent with this hypothesis.

The *winter female mimicry hypothesis* (Brown and Brown 1988) predicts that subadult male winter plumage should be equally or more adult female-like than the preceding fall plumage. The data strongly support this hypothesis because subadult males replace first prebasic plumage during presupplemental molt with a supplemental plumage that is identical in color to definitive female plumage (except for retained greater primary coverts).

The occurrence of this presupplemental molt raises an obvious question. Why do subadult males incur the energetic and potential predation costs of molt in order to replace an unworn first basic plumage with a supplemental plumage that is similar in structure and color? The most likely explanation is that by acquiring a supplemental plumage that is indistinguishable from definitive female basic plumage, first-year males may 1) suffer less predation than adult males, and/or 2) be mistakenly identified as adult females and thereby incur less aggression from adults.

As discussed above, subadult male Indigo Buntings undergo a presupplemental molt, usually on the wintering ground, resulting in a winter supplemental plumage that is adult male-like in color. As a result, Rohwer (1986) speculated that subadult male Indigo Buntings achieve sufficient experience after a month or two on the wintering ground to be able to dominate adult females and compete with adult males. As a result, selection may have favored the evolution of this molt as a mechanism for subadult males to acquire a new honest status signal which reflects their enhanced competitive ability. In contrast, I suggest that the average competitive ability attained by subadult male Painted Buntings on the wintering ground is inferior to that of adult males and females. Thus, selection may have favored subadult males to deceitfully mimic adult females by growing supplemental plumage that is adult female-like in color rather than to honestly signal subordination to adults by growing supplemental plumage that is juvenile-like in color. In addition, if the energetic cost of molting is less on the breeding ground or during migration than on the wintering ground (e.g., due to greater food availability), this may explain why presupplemental molt in subadults occurs before reaching the wintering ground in Painted Buntings but after reaching the wintering ground in Indigo Buntings.

If second-year males replace their first winter plumage with a less conspicuous summer plumage, this would support the winter status signaling hypothesis and be inconsistent with the winter cryptic and female mimicry hypotheses. Replacement of winter plumage with an equally or more conspicuous summer plumage would be consistent with all winter hypotheses. Since second-year males replace winter plumage with a nearly identical and adult female-like summer plumage during first prealternate molt, this is consistent with all three winter hypotheses.

#### SUMMER HYPOTHESES

The *summer status signaling hypothesis* (Lyon and Montgomerie 1986, Montgomerie and Lyon 1986) predicts that subadult male plumage color should reliably signal fighting ability. As discussed above, Painted Buntings are often multi-brooded (Parmelee 1959). As a result, during their first potential breeding season, subadult males vary greatly in their relative ages and, therefore, presumably in fighting ability as well. Thus, the

summer status signaling hypothesis predicts that the extent of adult male-like summer plumage exhibited by subadult males during their first potential breeding season should be correlated with male fighting ability and, therefore, should vary considerably among subadult males. In addition, the greater that the extent is, on average, of adult male-like plumage worn by subadult males during their first potential breeding season relative to the winter plumage that preceded it, the stronger is the support for this hypothesis. Replacement of winter plumage with an equally or more cryptic summer plumage by subadult males would be inconsistent with this hypothesis.

Subadult males 1) grow plumage during first prealternate molt that is almost exclusively adult female-like in color, and 2) exhibit remarkably little variation in plumage color among individuals. This is the first species documented in which sexually mature males usually grow adult female-like rather than male-like plumage during a prealternate molt. However, I recently have found that House Finches, *Carpodacus mexicanus*, in central Arizona also undergo a limited prealternate molt in which both second-year and older males replace adult male-like (red) feathers only with female-like (brown, rarely yellow) feathers (Thompson, unpub. data). This finding in Painted Buntings is inconsistent with the summer status signaling hypothesis. However, the strength of this conclusion is weakened because spring molt is limited in extent. This result does not necessarily imply that second-year males achieve greater lifetime inclusive fitness by wearing an adult female-like plumage in summer than they would if they wore an adult male-like plumage in summer. Instead, it may indicate that selection favors them to wear an adult female-like plumage because they are unable to attain a completely adult male-like plumage. In summer, selection may favor subadult males with plumages that are either relatively adult male-like or adult female-like, but not intermediate between the two. Thus, in species in which spring molt is limited, selection may favor subadult males that remain in adult female-like plumage by growing adult female-like feathers during spring molt, rather than subadult males that attain intermediate plumage by growing adult male-like feathers (Rohwer et al. 1980, 1983; Rohwer and Butcher 1988).

The *summer cryptic hypothesis* (Selander 1965, 1972; Proctor-Gray and Holmes 1981) would be

strongly supported if subadult males exhibit a late winter or spring molt resulting in a summer plumage that is more cryptic than their previous first winter plumage. However, as discussed above, the relative strength of this support depends on how extensive this molt is. The greater the increase in conspicuousness of plumage color exhibited by subadult males from winter to their first potential breeding season, the weaker is the support for this hypothesis. Because subadult males grow plumage during first prealternate molt that is adult female-like and not less conspicuous in color relative to their previous winter plumage, this is inconsistent with the summer cryptic hypothesis.

The *summer female mimicry hypothesis* (Rohwer et al. 1980, 1983; Rohwer 1983) would be strongly supported if subadult males exhibit a late winter or spring molt resulting in a summer plumage that is as or more adult female-like in color than their previous first winter plumage. Because subadult males grow plumage during first prealternate molt that is adult female-like in color, this strongly supports the summer female mimicry hypothesis. However, as discussed above, the relative strength of this support depends on how extensive this molt is. Because of the limitations of molt studies using museum skins, and because this molt does not cause a discernable change in plumage color or structure, except on the head in some subadult males, I could not accurately estimate the extent of this molt. To do so, one would have to perform a mark-recapture study on a wintering population.

The *juvenile mimicry hypothesis* (Lawton and Lawton 1986, Foster 1987) would be supported only if, during their first potential breeding season, second-year males wear a juvenile-like plumage and behave like juveniles, and would be refuted if they wear an adult male-like or adult female-like plumage, or if they exhibit aggressive reproductive behavior. The data are inconsistent with the hypothesis because the plumage of subadult males during their first potential breeding season resembles definitive female and not juvenile or first basic plumage, and because subadult male Painted Buntings often defend breeding territories and exhibit reproductive behavior similar to adult males (Lanyon and Thompson 1986, Thompson, unpub. data).

The *molt constraints hypothesis* (Rohwer and Butcher 1988) makes no predictions regarding plumage color of subadult males during their first

winter or first potential breeding season. However, it would be supported if subadult males molt less extensively than adult males during a late winter or spring molt. Conversely, a complete prebreeding body molt by subadult males would be inconsistent with the hypothesis. An equally extensive but incomplete prebreeding body molt by both subadult and adult males would suggest that such a molt is either physiologically constrained or selectively favored.

The frequency of prealternate molt does not differ between subadult and adult males. These results are consistent with but do not support the molt constraints hypothesis. However, the intensity of prealternate molt is greater in adult males than any other age or sex class. This result suggests that extent of first prealternate molt may be more energetically limited in subadult than adult males and, therefore, supports the molt constraints hypothesis.

As evidence in support of the molt constraints hypothesis, Rohwer (1986) documented that prealternate molt by subadult male Indigo Buntings often is continued on the breeding ground after spring migration. Rohwer proposes that in spring there is less competition for food on the breeding ground than the wintering ground because food is more abundant on the breeding than the wintering ground. As a result, first prealternate molt may be favored to continue on the breeding ground after spring migration. However, Painted Buntings undergo prealternate molt almost exclusively on the wintering ground, thus not supporting the molt constraints hypothesis.

If the extent of prealternate molt is limited by a constraint (e.g., food), then winter and summer plumages of Painted Buntings may not be functionally independent of one another. Thus, if subadult plumages in males are a greater fitness advantage in winter than a fitness disadvantage in summer, then supplemental plumage could be viewed as an adaptation to winter, and retention of adult female-like plumage in summer as making the best of a bad situation (Gross 1984). For example, when suitable breeding habitat is limited, and adult males outnumber reproductively mature females, subadult males are forced to compete with adult males for mates and territories. Under these or analogous circumstances in winter or summer, selection may favor subadult males that are either female-like or adult male-like in appearance, but not intermediate between the two (Rohwer et al. 1980, 1983; Roh-

wer and Butcher 1988). Rohwer et al. (1980) modeled the evolution of subadult male plumages and concluded that evolution of intermediate plumages should be rare. Two lines of evidence from this study support Rohwer et al.'s model. First, subadult males could wear a winter plumage that is intermediate in color between definitive male and female winter plumage and wear an adult female-like plumage in summer by replacing the adult male-like part of their winter plumage with adult female-like plumage during first prealternate molt. Second, because subadult male Painted Buntings grow adult female-like rather than adult male-like plumage during first prealternate molt, this suggests that they cannot undergo a sufficiently extensive prealternate molt to achieve a completely adult male-like appearance in summer. In turn, this suggests that selection may favor either a reduction in the extent of prealternate molt and/or growth of female-like rather than adult male-like first alternate plumage by subadult males. That subadult males could, but do not, wear a plumage in winter, summer, or both that is intermediate in color between definitive male and female plumage is the first empirical data that support Rohwer et al.'s (1980) model. However, in species with complex social systems, such as cooperative breeders, it is likely that young males of some species may molt into either a completely adult male-like plumage or a completely female-like plumage as suggested by Rohwer et al.'s model. For example, this may occur in Lovely Fairy Wrens, *Malurus amabilis*, a cooperatively breeding Australian passerine, in which Schodde (1982) states that "some young birds seem to change directly into [male] nuptial dress during the post-juvenile moult (e.g., Harrison 1974), while others colour up like old females, particularly if they are subordinate members of a communal group (K. A. Muller, pers. comm.)."

If subadult plumages in males are a greater fitness advantage in summer than a fitness disadvantage in winter, then adult female-like plumage could be viewed as adaptive in summer but potentially maladaptive in winter. In addition, selection may have favored the evolution of delayed plumage maturation during one season (winter or summer) only. Retention of subadult plumage during a season when it was initially maladaptive may have acted as a preadaptation for the evolution of a secondary function (e.g., status signaling, female mimicry) dur-

ing that season. In this way subadult male plumages may have become adaptive during both winter and summer.

The energetic cost of molt is poorly understood. Walsberg (1983) concludes from a survey of the literature that molting "represents the major event of somatic production during the annual cycle" and requires an increase in energy expenditure that "significantly affect[s] the energy relationship of free-living birds." Thus, molt is integrated in the annual cycle with reproduction and migration as one of the most socially and physiologically important and most energetically expensive events during the annual cycle. Unfortunately, as Rohwer and Butcher (1988) and Rohwer and Manning (1990) recently commented, qualitative and quantitative knowledge of the sequence, timing, location, and extent of molts is sorely lacking and desperately needed for the majority of birds worldwide. Such information about molt is essential for addressing many central questions in evolutionary biology and ecology regarding predation, intraspecific mimicry, thermoregulation, physiological constraints, and paedomorphosis among others. This study emphasizes that such information about molt can be extracted from museum specimens, and used to address questions regarding the evolution of delayed somatic maturation, molt strategies, and the integration of these life history traits with other life history parameters. Hopefully, this study will encourage others to address the evolution of delayed plumage maturation, as well as other central questions in biology, by doing similar studies on other relatively unstudied species. Most scientists have assumed that absence of seasonal change in plumage color indicates absence of molt. As mentioned above, fourteen species of North American passerines have subadult male plumages that differ very little between winter and summer (Table 1, category 3 in Rohwer and Butcher 1988). Of these species, only the Northern Oriole (Rohwer and Manning (1990), Painted Bunting (this study), and House Finch (Thompson, unpub. data) have been specifically investigated for the occurrence of a spring molt. This study indicates that absence of change in plumage color between winter and summer does not always indicate an absence of molt but, rather, may indicate growth of similarly colored plumage. This suggests that similar investigations of spring molt in the other 11 species, especially Purple Finches (*Carpodacus pur-*

*pureus*), Cassin's Finches (*C. cassinii*), Great Basin populations of House Finches, and Olive Warblers (*Peucedramus taeniatus*) are strongly warranted, and likely to further advance our understanding of the evolution of delayed plumage maturation.

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