

# DIFFERENCES IN TIMING AND NUMBER OF MOLTS FOR BALTIMORE AND BULLOCK'S ORIOLES: IMPLICATIONS TO HYBRID FITNESS AND THEORIES OF DELAYED PLUMAGE MATURATION<sup>1</sup>

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**Abstract.** We compare the molt and migration schedules of Baltimore (*Icterus g. galbula*) and Bullock's (*I. g. bullockii*) orioles, describe how *bullockii* and Black-backed Orioles (*I. g. abeillei*) in juvenile plumage can be distinguished, and present a simple quantitative character that serves to distinguish the juvenile and basic plumages of *bullockii*. *Galbula* undergoes the first and later prebasic molts on the breeding grounds, while *bullockii* in both juvenile and worn breeding plumage almost certainly migrate to the American southwest prior to undertaking the fall molts. This early migration by *bullockii* has probably been favored as a mechanism for them to escape the dry late summer conditions that prevail in most of their breeding range and to exploit for molting the food flush caused by the late summer monsoon rains in the southwest. With but one exception, every *bullockii* specimen taken in late summer or fall south of the breeding range in Mexico was in fresh basic plumage. Thus, the fall migration of *bullockii* may be interrupted for the prebasic molts.

*Bullockii* almost entirely lacks a prealternate molt in all sex and age classes. The prealternate molt in *galbula* is fairly extensive in first-year males but limited in females and in older males. First year *galbula* males initiate this molt in their throat in early winter, perhaps to acquire a badge that helps distinguish them from first-year females, which have light throats, and from those older females that have light throats. Some *galbula* males that are almost a year old also undergo part of the prealternate molt after their arrival on the breeding grounds. Implications of these observations for theories of subadult plumages are discussed.

These differences between *galbula* and *bullockii* in the timing of the fall molts relative to the fall migration and in having or not having a prealternate molt may provide strong sources of selection against hybrids. One specimen illustrating some of the potentially deleterious recombinations of molt and migration schedules among hybrids is described in detail.

**Key words:** *Icterus galbula*; molt; interrupted migration; delayed plumage maturation; molt migration; subadult plumage.

## INTRODUCTION

Molts are important energy-demanding events in the avian annual cycle and knowledge of the timing number and extent of molts is critical to interpreting many aspects of avian biology. Our knowledge of the molts of North American passerines is so poor that studies requiring knowledge as basic as whether or not a species has a prenuptial molt or whether a species molts before or after the fall migration are often foiled by a lack of descriptive and, especially, quantitative data (but see Pyle et al. 1987). Studies of molt constitute perhaps the single largest block of de-

scriptive data begging to be extracted from museum specimens, particularly of migratory species where capture and recapture of live birds in their various ranges is impractical and expensive. Using data taken entirely from museum collections, we here describe and discuss remarkable differences in the molts of Baltimore and Bullock's orioles (nomenclature below).

Throughout this paper we use the following names to distinguish three dramatically different semispecies, allospecies, or species of orioles having largely allopatric breeding ranges. *Galbula* refers to the "Baltimore" Oriole, *Icterus galbula galbula*; *bullockii* refers to the "Bullock's" Oriole, *I. g. bullockii* and *I. g. parvus* (AOU 1957); and, *abeillei* refers to the "Black-backed" Oriole, *I. g. abeillei*. The entire complex presently is treated as *Icterus galbula*, the Northern Oriole (AOU 1983), because of well-studied hybridiza-

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tion between *galbula* and *bullockii* in the Great Plains (Sutton 1938, Sibley and Short 1964, Rising 1970) and presumed, but insufficiently documented, hybridization between *bullockii* and *abeillei* in Durango (Miller 1906; Rising 1970, 1973). Along some river systems in the Great Plains, most adult males resemble either *galbula* or *bullockii* and apparent hybrids occur in low frequency (Rising 1973, Corbin and Sibley 1977, Edinger 1985), while along others most specimens taken near the center of the cline appear to be hybrids (Rising 1970, 1983a). At Crook, Colorado, near the center of the cline along the Platte River, Edinger (1985) has recently documented strongly assortative pairing that may be a consequence of active mate choice. In this paper we document differences between *galbula* and *bullockii* both in timing and in numbers of molts per year. These differences may seriously reduce the fitness of hybrids and could be the basis for prezygotic isolating mechanisms that may have produced the assortative pairing Edinger (1985) recently documented in Colorado. Apart from listing a set of criteria by which *bullockii* and *abeillei* specimens in juvenile plumage may be distinguished, this report contains little further information on *abeillei*.

Throughout this paper we follow the molt terminology of Humphrey and Parkes (1959). To refer to age classes of birds we largely follow the system used by the Bird Banding Laboratory with modifications similar to Pyle et al. (1987). We reserve juvenile (JUV) for birds in juvenile plumage and we restrict hatching year (HY) to specimens taken in their first calendar year of life but after completion of the first prebasic molt. Thus, HY birds were taken between the first prebasic molt and 31 December of the year they hatched. Starting 1 January males in their first year of life are referred to as second year (SY) males until the second prebasic molt is so advanced that they can no longer be distinguished from older birds (ASY, for after second year). We also apply the term subadult to HY and SY males that are either in their first basic or first alternate plumages, or a mix thereof; such males are more or less female-like in appearance. Subadults, then, are males between the first and definitive prebasic molts and they are less than fully adult in appearance.

Subadult male *galbula* usually assume a first breeding plumage intermediate between that of the dully colored females and conspicuously col-

ored males, while subadult male *bullockii* always resemble females in their first breeding plumage (Rohwer et al. 1980, this study). Because of their presumed close relationship we assumed that the molt cycles of *galbula* and *bullockii* would be similar. The original goal of this study was to compare the color of the feathers replaced by subadult males of the two forms in their first prealternate molt. This comparison was of interest because the growth of female-like feathers in the first prealternate molt would strongly suggest that having a female-like subadult plumage for the first potential breeding season was an adaptation for that season (see Rohwer et al. 1983, Rohwer 1986, and Rohwer and Butcher 1988).

To our surprise, however, the molt cycles of these birds proved to be very different. Indeed, *bullockii* appears to lack entirely a prealternate molt (see Fig. 1, which summarizes information from Sealy [1979, 1986] and the tables herein). This foiled our original goal, but stimulated us to describe the fundamental differences in the molts of these two forms. We do not describe the postbreeding molts for either form. For *galbula* the fall molts have already been described (Sealy 1979, 1986) and for *bullockii* so few specimens have been collected in either the first or definitive prebasic molt that descriptions of the extent, rate, and sequence of these molts would be premature.

This study has the following major implications, all of which are developed in the Discussion. First, while *galbula* undergoes its first and definitive prebasic molts on its breeding grounds, *bullockii* apparently migrates, immediately after breeding, to the southwest where it presumably exploits the productivity following late summer rainstorms to support these molts (Fig. 1). Second, this scheduling difference, as well as the lack of a prealternate molt in *bullockii*, may strongly disfavor hybrids between these two forms, a point illustrated by one interesting specimen. Finally, several features of the prealternate molt in *galbula* suggest that the subadult male plumage of this form may best be viewed as an adaptation for winter status signaling.

## METHODS

This study is based entirely on museum specimens taken throughout the range of *galbula* and *bullockii*, except that specimens from areas of potential hybridization were excluded. We examined 825 specimens of *bullockii* and 556 of

## HY and SY males/females

## SY and ASY males/females

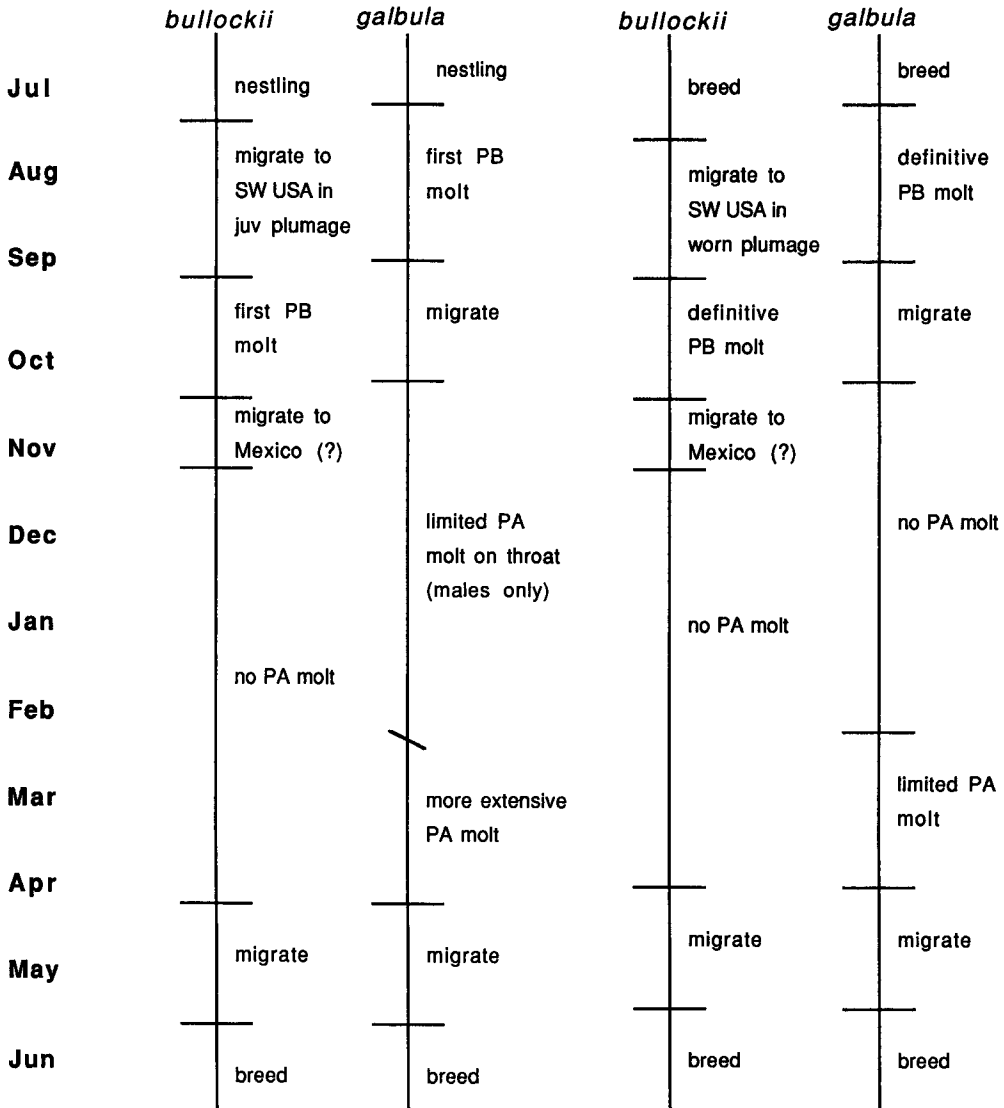


FIGURE 1. Schematic summary and comparison both of the number and timing of molts and of their scheduling relative to migration for Bullock's and Baltimore orioles.

*galbula* for molt, but only 561 *bullockii* and 303 *galbula* specimens were actually relevant to our tables. Manning scored most of the specimens for molt but we sorted them into age and species classes together.

## HYBRIDS

We attempted to exclude *galbula* × *bullockii* hybrids from most of our analyses. This was easiest

for males in definitive plumage because of their dramatic plumage differences and because one of us (Rohwer) also scored most of the winter-taken adult males using Rising's (1970) hybrid index. This index ranges from 0 to 29; birds falling from 5 to 24 were excluded from our tables. Hybrids of females and subadult males are more difficult to recognize but we excluded any obvious hybrids. Even if some have been included,

TABLE 1. Frequencies of specimens vs. numbers of barbs along the terminal 10 mm of one vane of juvenile and first basic body feathers from the lower flanks of *I. g. bullockii*.

| Plumage generation            | Number of barbs |   |    |    |    |    |    |    |    |    |    |    |
|-------------------------------|-----------------|---|----|----|----|----|----|----|----|----|----|----|
|                               | 8               | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
| Juvenile plumage (♂♂ and ♀♀)  | 1               | 1 | 12 | 11 | 8  | 3  | 0  | 0  | 0  | 0  | 0  | 0  |
| First basic plumage (♂♂ only) | 0               | 0 | 0  | 0  | 0  | 3  | 2  | 8  | 8  | 9  | 5  | 1  |

the bias they generate should be negligible because they would constitute only a tiny fraction of the specimens examined. The extensive series of *galbula* and *bullockii* collected for studies of introgression between these birds were excluded from this study.

#### DISTINGUISHING JUVENILE AND BASIC PLUMAGES

To assist in categorizing fall *bullockii* into either juvenile or basic plumage we have quantified the difference in numbers of barbs on the longest feathers of the flanks (Table 1). This work was done under a dissecting microscope using 8× magnification. A long and undamaged lower flank feather was isolated and pressed flat against a millimeter ruler. The ruler was positioned such that the distal-most barb easily seen under 8× magnification was at 0. This barb was usually about 1 mm back from the end of the feather shaft. The barbs forming one side of the feather vane were then counted along the next 10-mm length of the feather shaft. The last barb was included if it was closer to the 10-mm mark than one-half of the distance between it and the next barb.

For these barb counts, specimens were considered to be in basic plumage if they had been taken after 1 November; as we show below, the first prebasic molt is complete before this date. Specimens were considered to be in juvenile plumage if they were taken on the breeding grounds in July or August and also had either growing rectrices or labels indicating the presence of incompletely pneumatized skulls.

#### SCORING MOLT

Body molt was scored in six regions: (1) throat, the anterior undivided portion of the ventral tract; (2) breast, the middle portion of the ventral tract immediately anterior and posterior to its bifurcation; (3) belly, the posterolateral branches of the ventral tracts, including the flanks and belly feathers; (4) crown, the capital tract covering the

top of the head; (5) back, the anterior and central region of the dorsal tract; and (6) rump, the posterior section of the dorsal tract immediately above the tail. Body feathers were lifted with forceps at five to 10 points in each of these regions to check for the presence of feathers that had been in active growth when the specimen was collected. For each body region molt scores were assigned as follows: 0 = no active molt, 1 = one to two growing feathers, 2 = three to four growing feathers and 3 = five or more growing feathers. Concentrated and asymmetrical patches of incoming feathers of the same age were not scored as molt since such feather growth was likely due to accidental losses of feathers.

The molt scores for the six body regions were summed to give a Total Body Molt (TBM) score for each specimen. With the exception of Tables 6 and 7 showing the intensity of molt, specimens having TBM scores of 1.0 were excluded from our analyses because of the possibility that the presence of just one or two feathers growing in a single body region might only represent the replacement of pulled feathers. This convention was not followed in Tables 6 and 7 because fall specimens showing TBM scores of 1.0 always were replacing feathers on their throats, suggesting a real, but low intensity molt.

Since our "active molt scores" do not distinguish between specimens just beginning or almost finished with their molt, we also noted how much of the plumage was fresh. This information helped categorize specimens in Tables 2–4.

Primaries, secondaries, and rectrices were counted on every specimen and missing or growing feathers recorded. The relative length of incoming feathers in these tracts was scored on a 1 to 5 scale where 1 = pin or brush, 2 = a feather less than 25% of full length, 3 = 25–50% of full length, 4 = 51–75% of full length, and 5 = more than 75% of full length but still growing. So few *bullockii* specimens exhibited growing remiges or rectrices that we report only on the presence or absence of molt of these feathers.

## DEFINITIONS OF BREEDING AND WINTER RANGES

To summarize the scheduling of the fall molts relative to the fall migration we categorized specimens in most tables as taken either in or south of the breeding range. This creates a relatively clean dichotomy for *galbula* since they breed entirely in the United States and Canada and winter largely in Mexico and Central America. To avoid confusion we eliminated the few midwinter specimens from the United States except where noted. Breeding and winter ranges overlap for *bullockii* in southern California, Arizona, New Mexico, and the northern states of Mexico. All specimens from the United States, Sonora, Chihuahua, and Coahuila were considered to be on their breeding grounds and specimens from Sinaloa and Durango were divided into "breeding" or "wintering" according to whether or not they had been taken south of known breeding localities. The few specimens that we examined from Baja California were eliminated. This procedure results in an extremely conservative definition of the winter range of *bullockii*. We have resolved this difficulty in tables addressing the geographic location and timing of their fall molts by providing, in footnotes, the collecting localities of critical specimens; most were taken in the zone in which breeding and winter ranges overlap.

## RESULTS

### DISTINGUISHING JUVENILE AND BASIC PLUMAGE

Orioles in full juvenile plumage are difficult for some workers to distinguish from females in fresh basic plumage and from subadult males in first basic plumage. This is particularly troublesome in *bullockii* because HY birds undergo much of the fall migration prior to molting. Consequently, females and subadult males that are in fresh basic plumage and HY birds in full juvenile plumage may be found together in late summer and early fall in the northern part of their winter range.

The juvenile and basic plumages of *galbula*, *bullockii*, and *abeillei* are readily distinguished by the laxity of the feather vanes, particularly on the flanks. The feathers of the juvenile plumage have both a reduced number of barbs and barbs that are less well interlocked. This results in a plumage that, in gross appearance, is more lax, or softer and fluffier, than that of birds either in

worn breeding plumage or in fresh basic plumage. For *bullockii* we have quantified the difference between the juvenile and basic plumage with respect to number of barbs on the longest feathers of the lower flanks, an area where feather texture differences are most apparent (Table 1). Despite some overlap (much of which was probably caused by choosing feathers of somewhat different lengths for barb counts) differences in these counts are strong. Mid-values are 11 barbs per side per 10 mm of feather shaft for juvenile flank feathers and 16 for basic feathers (Table 1).

### DISTINGUISHING *ABEILLEI* AND *BULLOCKII* JUVENILE PLUMAGE

We found a considerable number of *abeillei* specimens in juvenile plumage that had been misidentified as *bullockii*. Because the winter ranges of *bullockii* and *abeillei* overlap and because *bullockii* undergoes its fall molts after undertaking at least part of the fall migration, correct identification of these forms is critical to a proper analysis of the scheduling of the first prebasic molt of *bullockii*. We were able to distinguish these forms in juvenile plumage by the following characters. *Abeillei* juveniles are generally darker in tone than *bullockii*, especially ventrally. This is particularly evident on the flanks, which in *abeillei* juveniles are a brownish-gray but which in *bullockii* juveniles are a pale silvery-gray, scarcely contrasting with the belly. In *abeillei* juveniles the throat and breast are a rich yellow suffused with olive green, while the throat and breast of *bullockii* juveniles are usually very pale yellow and lack any greenish tinge. In *abeillei* juveniles the crown color contrasts with the back because of its darker olive shade, while in *bullockii* juveniles the crown usually matches the back. Finally, in *abeillei* juveniles the auriculars are a medium dark yellowish-olive, matching the crown in color, whereas these feathers are a light to golden yellow matching the color of the throat in *bullockii*.

### TIMING OF THE PREBASIC MOLTS

The prebasic molts of *galbula* have long been known to occur on the breeding grounds (Dwight 1900, Forbush 1924, Roberts 1974, Sealy 1979). Sealy (1979) reported that SY males began molting at the same time as females (a few days before adult males) but that SY males may begin moving southward early in the molt. The second prebasic molt (as well as all other prebasic molts)

TABLE 2. Geographic location and timing of the first prebasic molt in male *I. g. bullockii*.

|     |       | Specimens mostly or entirely in juvenile plumage |             |                   |             | Specimens mostly or entirely in first basic plumage |                |                   |             |
|-----|-------|--|-------------|-------------------|-------------|---|----------------|-------------------|-------------|
|     |       | Breeding grounds                                 |             | Wintering grounds |             | Breeding grounds                                    |                | Wintering grounds |             |
|     |       | Molting  | Not molting | Molting           | Not molting | Molting   | Not molting    | Molting           | Not molting |
| Jun | 1-15  | 0  | 0           | 0                 | 0           | 0   | 0              | 0                 | 0           |
|     | 16-30 | 0  | 2           | 0                 | 0           | 0   | 0              | 0                 | 0           |
| Jul | 1-15  | 1 <sup>a</sup>                                   | 12          | 0                 | 0           | 0   | 0              | 0                 | 0           |
|     | 16-31 | 0  | 17          | 0                 | 0           | 0   | 0              | 0                 | 0           |
| Aug | 1-15  | 1 <sup>b</sup>                                   | 24          | 0                 | 0           | 0   | 0              | 0                 | 0           |
|     | 16-31 | 0  | 18          | 0                 | 0           | 0   | 0              | 0                 | 0           |
| Sep | 1-15  | 0  | 0           | 0                 | 0           | 1 <sup>c</sup>                                      | 0              | 0                 | 3           |
|     | 16-30 | 0  | 0           | 0                 | 0           | 2 <sup>d</sup>                                      | 0              | 0                 | 2           |
| Oct | 1-15  | 0  | 0           | 0                 | 0           | 0   | 0              | 0                 | 7           |
|     | 16-31 | 0  | 0           | 0                 | 0           | 0   | 2 <sup>e</sup> | 0                 | 2           |

<sup>a</sup> UAZ 9833 San Diego County, California (TBM = 7).

<sup>b</sup> USNM 413417 Okanagan Lodge, British Columbia (TBM = 2).

<sup>c</sup> UCLA 29279 Saric, Sonora (TBM = 18, all greater secondary coverts growing).

<sup>d</sup> USNM 480713 Scottsdale, Arizona (TBM = 12, growing S8 and 9, all greater secondary coverts new); UAZ 5147 San Xavier Mission, Arizona (TBM = 9, also growing outer rectrices).

<sup>e</sup> MVZ 164647 Wilmington, (Southern) California; LSU 100515 Cameron Parish, Louisiana.

must be completed in breeding latitudes as we found no specimen that had arrived in Central America with remnants of worn subadult (or juvenile or adult) plumage.

Unlike *galbula*, both juvenile and adult *bullockii* apparently undertake most of the fall migration prior to the prebasic molt (Fig. 1). Unfortunately, this conclusion is based largely on negative data concerning the numbers of molting and nonmolting specimens collected on the breeding or wintering grounds (Tables 2 and 3 for males and Table 4 for females). Despite examining most of the specimens available in skin collections located in the United States and Canada (see Acknowledgments), we found only 22 *bullockii* specimens in any stage of either the first or definitive prebasic molts. Of these 22 specimens, 17 were taken in the area of overlap between the breeding and wintering ranges (southwestern United States and northern Mexico) and five were taken north of this area at localities where *bullockii* breeds but does not winter. Just 11 of the 22 molting specimens had total body molt scores of 5 or more (maximum possible = 18) and 10 of these 11 specimens in moderate to heavy molt were taken in the southwest. The 11th was of the five more northerly specimens and was taken in the hybrid zone in Oklahoma (see Table 3); although not a hybrid by plumage, this bird could have been molting there because of *galbula* genes affecting its nonplumage characters. Because *bullockii* has overlapping breeding and winter ranges, the collecting localities of

the 22 molting specimens argue only weakly that *bullockii* migrates before undergoing its fall molts. This thesis, however, is further supported by three additional arguments.

First, *bullockii* is a very early fall migrant, generally arriving on the Farallon islands (west of San Francisco) in mid-July and peaking in early to mid-August (DeSante and Ainley 1980). Since *bullockii* nests in May and June, and since we saw no specimen suggesting that they might molt while breeding, these early migration dates virtually preclude a molt occurring prior to the migration. Second, many specimens exist that were taken north of known wintering areas in late summer and that were not in molt. For birds in juvenile plumage we examined 73 such specimens from August and September (Tables 2 and 4). For adults, which apparently migrate earlier than juveniles (see Tables 2, 3, and 4), we examined 58 worn specimens from July and August that were not in molt, but none from September (Tables 3 and 4). If the first or definitive prebasic molts occurred on the breeding grounds, many of these specimens that were late to migrate should have been in molt. Finally, a number of specimens taken while in full juvenile plumage bear labels indicating that they were either in migration or preparing to migrate when collected. Steve Cardiff took five such specimens on 13 August and two more on 30 August near Baker in southern California at a locality where Bullock's Orioles do not nest (LSU 126577-126583); four were carrying moderate or larger

TABLE 3. Geographic location and timing of the definitive prebasic molt in male *I. g. bullockii*.

|     |       | Specimens mostly or entirely in worn basic plumage (subadults and adults) |             |                   |                | Specimens mostly or entirely in fresh definitive basic plumage (all adults) |                |                   |             |
|-----|-------|---|-------------|-------------------|----------------|---|----------------|-------------------|-------------|
|     |       | Breeding grounds  |             | Wintering grounds |                | Breeding grounds  |                | Wintering grounds |             |
|     |       | Molting   | Not molting | Molting           | Not molting    | Molting   | Not molting    | Molting           | Not molting |
| Jun | 1-15  | 0   | 21          | 0                 | 0              | 0   | 0              | 0                 | 0           |
|     | 16-30 | 0   | 18          | 0                 | 0              | 0   | 0              | 0                 | 0           |
| Jul | 1-15  | 5 <sup>a</sup>  | 25          | 0                 | 0              | 0   | 0              | 0                 | 0           |
|     | 16-31 | 2 <sup>b</sup>  | 8           | 0                 | 0              | 0   | 0              | 0                 | 0           |
| Aug | 1-15  | 0   | 0           | 0                 | 0              | 0   | 0              | 0                 | 0           |
|     | 16-31 | 0   | 0           | 0                 | 0              | 0   | 0              | 0                 | 1           |
| Sep | 1-15  | 0   | 0           | 0                 | 1 <sup>c</sup> | 1 <sup>d</sup>  | 1 <sup>e</sup> | 0                 | 0           |
|     | 16-30 | 0   | 0           | 0                 | 0              | 2 <sup>f</sup>  | 1 <sup>g</sup> | 0                 | 2           |
| Oct | 1-15  | 0   | 0           | 0                 | 0              | 0   | 1 <sup>h</sup> | 0                 | 7           |
|     | 16-31 | 0   | 0           | 0                 | 0              | 1 <sup>i</sup>  | 1 <sup>j</sup> | 0                 | 11          |

<sup>a</sup> USNM 194897 Marysville Buttes, (N. Central) California (TBM = 2); USNM 205667 Winslow, Arizona (TBM = 2); USNM 205668 Winslow, Arizona (TBM = 3); USNM 262057 Grand Dalles, Washington (TBM = 2); UCLA 29009 Saric, Sonora (TBM = 3).

<sup>b</sup> USNM 194685 Tres Piedras, New Mexico (TBM = 2); USNM 481935 Scottsdale, Arizona (TBM = 2).

<sup>c</sup> Moore 10265 Motzorongo, Veracruz (worn breeding plumage).

<sup>d</sup> MVZ 143908 Chihuahua (TBM = 12, also growing primaries, secondaries, and rectrices).

<sup>e</sup> MVZ 119777 Ramos, Chihuahua (outermost primary full length but sheathed at base).

<sup>f</sup> San Diego 33634 Bard, (southern) California (TBM = 6, remiges and rectrices new); USNM 575332 Kenton, Oklahoma (TBM = 4, remiges and rectrices new; much fat). Kenton, Oklahoma is in the heart of the hybrid zone so, although the plumage score of this specimen places it in the range of *bullockii*, it may be *galbula*-like in some nonplumage characteristics.

<sup>g</sup> San Diego 33636 Bard, (southern) California.

<sup>h</sup> Moore 4079 Gaumuchil, Sinaloa.

<sup>i</sup> DMNH 34852 Nogales, Sonora (TBM = 9; completing primary, secondary, and rectrix molt).

<sup>j</sup> LSU 94272 Cameron Parish, Louisiana.

amounts of fat. Cardiff reports that these specimens and a number of others that he did not collect were associated with more than 30 other species of transients, none of which breed at this locality. Another specimen taken in Washington on 14 August (UWBM 37457) showed greater than moderate fat and was among a large number of migrants of other species moving along a brushy, desert water course, uncharacteristic of breeding habitat. An additional eight specimens all in full juvenile plumage were taken in Washington (UWBM uncataloged) along another desert water course from 16-18 August; they were associated with various other migrants and all were categorized as moderately fat to very fat (McCabe 1943). Finally, a specimen collected on 20 August in Socorro, New Mexico by van Rossem (UCLA 34260), carries a label notation "desert scrub-migrant." In particular, the substantial amount of fat in the nine Washington specimens that were taken in mid-August in full juvenile plumage leaves little doubt that they would have migrated before molting; there are practically no September records of Bullock's Oriole for Washington or British Columbia (Cannings et al. 1987).

In ensemble, the preceding data strongly suggest that most *bullockii* from northern latitudes undergo a substantial southward movement be-

fore they molt. Less clear is whether the migration is interrupted for the fall molts or whether it is usually completed prior to the initiation of these molts. Because eight of the nine specimens (all males; Tables 2 and 3) taken south of the breeding range in August or September had completed the fall molt, we think most *bullockii* arrest their migration to molt in the southwest before moving further south. But this conclusion remains tentative for two reasons. First, the extremely low numbers of specimens taken in August or September from areas south of the breeding range (we found only nine; Tables 2, 3, and 4) could be due either to an absence of birds or to a general lack of collecting in Mexico in late summer when *bullockii* would be molting. Second, one adult (ASY) male (Moore 10265; Table 3) has been taken in early September in worn breeding plumage in Veracruz; this bird may have migrated all the way to its winter range prior to undergoing its prebasic molt.

#### PROGRESSION AND TIMING OF THE PREBASIC MOLTS IN *BULLOCKII*

Given the limited number of *bullockii* specimens that have been collected in the fall molts, little can be said of the progression of these molts. We have provided details on these molting specimens in Tables 2-4. Only 11 of the 22 molting

TABLE 4. Geographic location and timing of the first and later prebasic molts in female *I. g. bullockii*.

|     | Specimens mostly or entirely in juvenile plumage |                |                   |             | Specimens mostly or entirely in worn basic plumage |                |                   |             | Specimens mostly or entirely in fresh basic plumage |                |                   |             |    |
|-----|--|----------------|-------------------|-------------|--|----------------|-------------------|-------------|---|----------------|-------------------|-------------|----|
|     | Breeding grounds                                 |                | Wintering grounds |             | Breeding grounds                                   |                | Wintering grounds |             | Breeding grounds                                    |                | Wintering grounds |             |    |
|     | Molting  | Not molting    | Molting           | Not molting | Molting  | Not molting    | Molting           | Not molting | Molting   | Not molting    | Molting           | Not molting |    |
| Jun | 1-15   | 0              | 1                 | 0           | 0  | 0              | 8                 | 0           | 0   | 0              | 0                 | 0           | 0  |
|     | 16-30  | 0              | 1                 | 0           | 0  | 0              | 9                 | 0           | 0   | 0              | 0                 | 0           | 0  |
| Jul | 1-15   | 0              | 6                 | 0           | 0  | 0              | 11                | 0           | 0   | 0              | 0                 | 0           | 0  |
|     | 16-31  | 0              | 11                | 0           | 0  | 1 <sup>a</sup> | 9                 | 0           | 0   | 0              | 0                 | 0           | 0  |
| Aug | 1-15   | 0              | 13                | 0           | 0  | 2 <sup>b</sup> | 3                 | 0           | 0   | 0              | 0                 | 0           | 0  |
|     | 16-31  | 0              | 13                | 0           | 0  | 1 <sup>c</sup> | 2                 | 0           | 0   | 0              | 0                 | 0           | 0  |
| Sep | 1-15   | 1 <sup>d</sup> | 4                 | 0           | 0  | 0              | 0                 | 0           | 0   | 0              | 2 <sup>e</sup>    | 0           | 0  |
|     | 16-30  | 0              | 1                 | 0           | 0  | 0              | 0                 | 0           | 0   | 0              | 1 <sup>f</sup>    | 0           | 0  |
| Oct | 1-15   | 0              | 0                 | 0           | 0  | 0              | 0                 | 0           | 0   | 1 <sup>g</sup> | 0                 | 0           | 2  |
|     | 16-31  | 0              | 0                 | 0           | 0  | 0              | 0                 | 0           | 0   | 0              | 0                 | 0           | 10 |

<sup>a</sup> UCLA 29047 Saric, Sonora (TBM = 2, beginning primary and secondary molt).

<sup>b</sup> USNM 397271 Lewiston, Idaho (TBM = 6, also growing primaries); USNM 481936 Scottsdale, Arizona (TBM = 0, growing primaries).

<sup>c</sup> UCLA 29182, Saric, Sonora (TBM = 16, also growing primaries, secondaries, and rectrices).

<sup>d</sup> USNM 184701 Castle Mountains, (western) Texas (TBM = 18).

<sup>e</sup> Moore 11712 Guirocoba, Sonora; UCLA 29278 Saric, Sonora.

<sup>f</sup> Moore 4075 Guirocoba, Sonora.

<sup>g</sup> MVZ 3882, San Diego County, California (TBM = 10, first prebasic molt).

specimens were in intense molt (TBM scores of 5 or more and, for adults, growing primaries). Most of these intensely molting specimens were taken in August and September (Tables 2-4).

#### PREALTERNATE MOLT IN *GALBULA* AND *BULLOCKII*

Four general points are made in this section concerning the prealternate molt: (1) it is lacking or extremely limited in *bullockii* (Fig. 1), (2) there is an age class contrast in its intensity in *galbula*, (3) it commences in HY male *galbula* in early fall, soon after their arrival on the wintering grounds, and (4) it may be continued on the breeding ground by subadult (SY) male *galbula* in spring (this point excluded, for simplicity, from Fig. 1).

Table 5 summarizes our data on the incidence of specimens collected in active prealternate molt on their wintering grounds. The difference between *galbula* and *bullockii* is striking. In February, March, and April, 38 of 47 SY male *galbula* (81%) were in prealternate molt whereas only three of 25 SY male *bullockii* (12%) were in molt ( $\chi^2 = 31.6$ ,  $P < 0.001$ ). In this same time period nine of 53 adult male *galbula* (17%) were molting, but only one of 61 adult male *bullockii* (2%) were molting ( $\chi^2 = 8.6$ ,  $P < 0.01$ ); for females four of 31 *galbula* (13%) were molting, but none of 49 *bullockii* were doing so ( $\chi^2 = 4.1$ ;  $P < 0.05$ ). This difference between *galbula* and *bullockii*

is even more striking when average intensity scores are compared for the prealternate molt. For these same months the 40 *galbula* subadults in active molt had an average total body molt score of 7.4 while the four *bullockii* specimens in active molt had an average score of 1.7 (Table 6;  $P < 0.01$  Mann-Whitney *U*-test using raw data).

In *galbula*, subadult (SY) males show both a higher frequency and a higher intensity of molt in spring than do adult (ASY) males (Tables 5 and 6). Females are comparable to adult males (Table 5) in the frequency of specimens exhibiting prealternate molt. Although SY and ASY females cannot be distinguished with certainty, the low frequency of molting females suggests that the prealternate molt is less extensive in SY females than it is in SY males.

In subadult male *galbula* the prealternate molt only rarely includes all body feathers and the degree to which it is incomplete accounts for the variability in appearance among subadult males (Rohwer et al. 1980, Flood 1984). In subadult males this molt is initiated in the throat and always is heaviest in the throat (Table 7). Young males from the wintering grounds that have initiated this molt prior to December are not completing the first prebasic molt because the texture of their feathers matches that of the first basic plumage. In midwinter this molt is extended to other major feather groups, but anterior regions



TABLE 5. Percentage of *I. g. galbula* and *I. g. bullockii* specimens taken on the wintering grounds while in active prealternate molt.<sup>a</sup>

|     |       | Subadult ♂♂ <sup>b</sup> |               |                  |               | Adult ♂♂       |               |                  |               | Females        |               |                  |               |
|-----|-------|--------------------------|---------------|------------------|---------------|----------------|---------------|------------------|---------------|----------------|---------------|------------------|---------------|
|     |       | <i>galbula</i>           |               | <i>bullockii</i> |               | <i>galbula</i> |               | <i>bullockii</i> |               | <i>galbula</i> |               | <i>bullockii</i> |               |
|     |       | % molting                | No. specimens | % molting        | No. specimens | % molting      | No. specimens | % molting        | No. specimens | % molting      | No. specimens | % molting        | No. specimens |
| Sep | 1-15  | 0                        | 3             | 0                | 3             | 50             | 2             | 0                | 0             | —              | 0             | —                | 0             |
|     | 16-30 | 0                        | 6             | 0                | 2             | 20             | 5             | 0                | 2             | —              | 0             | —                | 0             |
| Oct | 1-15  | 22                       | 9             | 0                | 7             | 0              | 12            | 0                | 7             | 25             | 4             | 0                | 2             |
|     | 16-31 | 14                       | 7             | 0                | 2             | 0              | 7             | 0                | 11            | 14             | 7             | 0                | 10            |
| Nov | 1-15  | 0                        | 7             | 0                | 2             | 0              | 11            | 0                | 10            | 0              | 5             | 0                | 2             |
|     | 16-30 | 0                        | 2             | 0                | 2             | 0              | 4             | 0                | 1             | 25             | 4             | 0                | 5             |
| Dec | 1-15  | 100                      | 1             | 0                | 5             | 0              | 9             | 0                | 12            | 0              | 5             | 0                | 9             |
|     | 16-31 | 29                       | 7             | 33               | 3             | 0              | 3             | 0                | 6             | 0              | 2             | 0                | 6             |
| Jan | 1-15  | 20                       | 5             | 0                | 2             | 17             | 12            | 0                | 14            | 0              | 8             | 0                | 3             |
|     | 16-31 | 0                        | 5             | 0                | 6             | 0              | 10            | 0                | 7             | 0              | 6             | 0                | 8             |
| Feb | 1-15  | 75                       | 8             | 0                | 4             | 11             | 9             | 0                | 14            | 0              | 4             | 0                | 6             |
|     | 16-29 | 89                       | 9             | 25               | 8             | 23             | 13            | 0                | 20            | 17             | 6             | 0                | 10            |
| Mar | 1-15  | 86                       | 7             | 0                | 5             | 0              | 11            | 0                | 5             | 0              | 4             | 0                | 10            |
|     | 16-31 | 94                       | 16            | 33               | 3             | 18             | 11            | 0                | 8             | 38             | 8             | 0                | 15            |
| Apr | 1-15  | 50                       | 4             | 0                | 5             | 43             | 7             | 10 <sup>c</sup>  | 10            | 0              | 7             | 0                | 7             |
|     | 16-30 | 67                       | 3             | —                | 0             | 0              | 2             | 0                | 4             | 0              | 2             | 0                | 1             |
| May | 1-15  | 100                      | 1             | 0                | 2             | —              | 0             | —                | 0             | 50             | 2             | 0                | 1             |
|     | 16-31 | —                        | 0             | 0                | 3             | —              | 0             | —                | 0             | 0              | 1             | 0                | 1             |

<sup>a</sup> For *galbula* all birds on the wintering grounds were included; for *bullockii* worn and molting birds from the wintering grounds from September and October were excluded as these were considered to be taken prior to or during the prebasic molt; the two *galbula* adult males that were molting in September were probably early migrants finishing their prebasic molt.

<sup>b</sup> HY and SY males.

<sup>c</sup> Moore 26893 with a hybrid score of 26 (Rising 1970); birds with scores from 5-24 were excluded.

of the body are always emphasized. Replacement of body feathers is least likely on the rump and flanks (Table 7). About 75% of SY males replace some or all of secondaries 7-9, with secondaries 8 and 9 often being replaced, and secondary 7 rarely so. Some rectrices may also be replaced in this molt. The prealternate molt does not, however, include any primaries or any of the outer series of secondaries (1-6) (exception: USNM 441283 taken on 9 April with all secondaries and primaries 1-5 replaced).

A remarkable feature of the prealternate molt in *galbula* is its seasonal extent (Fig. 1; Tables 5, 6, and 7). This is best seen in Table 6 where, unlike our other tables, we have included specimens having total body molt scores of 1.0. We did so because almost all of the September-February specimens in prealternate molt were molting on their throats. Although many of these scores were only 1.0, this many low scores concentrated in a single body region in fall and early winter suggests an organized feather replacement rather than adventitious loss. The consequence of this fall and early winter feather replacement is that subadult males taken on the wintering

grounds between 15 September and 31 January have significantly more black feathers on their throats ( $\bar{x} = 8.5$ ,  $n = 6$ ) than do fall subadults (HY) from the United States ( $\bar{x} = 2.5$ ,  $n = 25$ ) ( $P < 0.04$ , two-tailed Mann-Whitney *U*-test).

For 28 specimens of subadult *galbula* taken between 1 December and 30 April on the wintering ground we were able to determine the color of partially ensheathed feathers. In all but one of these specimens, all growing feathers resembled those of the adult male plumage; the exceptional specimen (CMNH 27687) showed some growing feathers in its face and throat that were a mix of orange and black, but most of its many growing feathers were fully adult in appearance. These 28 specimens suggest that fully female-like feathers are never grown by males in their first prealternate molt. One additional specimen (LSU 13902), also sexed as a male, showed incoming female-like feathers in most body regions. Because this is a unique specimen we assume it was either missexed or abnormal.

The prealternate molt in SY males of *galbula* frequently appears either to be resumed on the breeding grounds after the spring migration or

TABLE 6. Intensity of prealternate molt in *I. g. galbula* and *I. g. bullockii* males taken south of their breeding ranges and showing active molt.<sup>a</sup>

|     |       | Subadults      |             |                  |             | Adults         |             |                  |                |
|-----|-------|----------------|-------------|------------------|-------------|----------------|-------------|------------------|----------------|
|     |       | <i>galbula</i> |             | <i>bullockii</i> |             | <i>galbula</i> |             | <i>bullockii</i> |                |
|     |       | Average score  | No. molting | Average score    | No. molting | Average score  | No. molting | Average score    | No. molting    |
| Sep | 1-15  | —              | 0           | —                | —           | 4.0            | 1           | —                | —              |
|     | 16-30 | 1.0            | 2           | —                | —           | 3.0            | 1           | —                | —              |
| Oct | 1-15  | 2.0            | 2           | —                | —           | —              | 0           | —                | —              |
|     | 16-31 | 2.0            | 1           | —                | —           | —              | 0           | —                | —              |
| Nov | 1-15  | 1.0            | 4           | —                | 0           | —              | 0           | —                | 0              |
|     | 16-30 | 1.0            | 1           | —                | 0           | —              | 0           | —                | 0              |
| Dec | 1-15  | 4.0            | 1           | —                | 0           | 1.0            | 1           | —                | 0              |
|     | 16-31 | 2.3            | 3           | 2.0              | 1           | —              | 0           | —                | 0              |
| Jan | 1-15  | 5.0            | 1           | —                | 0           | 2.0            | 2           | —                | 0              |
|     | 16-31 | —              | 0           | —                | 0           | 1.0            | 2           | —                | 0              |
| Feb | 1-15  | 5.2            | 6           | 1.0              | 1           | 3.0            | 1           | —                | 0              |
|     | 16-29 | 4.4            | 8           | 2.0              | 2           | 2.0            | 4           | —                | 0              |
| Mar | 1-15  | 8.7            | 6           | —                | 0           | —              | 0           | —                | 0              |
|     | 16-31 | 9.9            | 15          | 2.0              | 1           | 7.3            | 3           | —                | 0              |
| Apr | 1-15  | 4.3            | 3           | —                | 0           | 2.2            | 5           | 3.0 <sup>b</sup> | 2 <sup>b</sup> |
|     | 16-30 | 7.5            | 2           | —                | 0           | —              | 0           | —                | 0              |
| May | 1-15  | 8.0            | 1           | —                | 0           | —              | 0           | —                | 0              |
|     | 16-31 | —              | 0           | —                | 0           | —              | 0           | —                | 0              |

<sup>a</sup> Unlike frequency tables, this table includes specimens with molt scores of 1.0; molting specimens of *bullockii* from September and October were excluded as being in prebasic molt; the two *galbula* adult males that were molting in September were probably early migrants finishing their prebasic molt.

<sup>b</sup> One of these two specimens had a molt score of 1.0. The other, Moore 26893, had a molt score of 5.0 and may have been of hybrid origin; its hybrid score was 26 (Rising 1970); all specimens with scores from 5-24 were excluded as hybrids.

to be continued through the migration. We examined 19 April–May specimens from the United States, all taken well north of sites where *galbula* occasionally winters; eight (42%) showed active body molt. The mean total body molt score for these eight specimens was 3.1 ( $\pm 1.64$ ). Not one of the 30 adult male and 17 female *galbula* that we examined from the United States in April and May was molting.

We have also documented a virtually complete absence of prealternate molting in early spring specimens of *bullockii* from the breeding grounds. We examined 45 SY males, 100 ASY males, and 46 females taken between 16 March and 30 May. Of these, only two SY males, one female, and one ASY male were molting, each having a total body molt score of 1.0.

## DISCUSSION

### SCHEDULING OF FALL MOLTS AND MIGRATION

Why should most *bullockii* apparently make a substantial southward migration prior to undergoing either the first or definitive prebasic molts, while *galbula* always delays the fall mi-

gration until these molts are complete or nearly complete (Fig. 1)? Most migratory passerines undergo the postbreeding molts prior to the fall migration. Many species of North American swallows and flycatchers, however, undergo their fall molts on the wintering grounds, after the fall migration (Dwight 1900, Johnson 1963, Niles 1972). The differences among species in these groups, as well as the differences between *galbula* and *bullockii* reported here, suggest that the timing of the fall molts relative to the fall migration is an evolutionarily labile character. This lability is further supported by species specific differences among age classes in the timing of the fall molt relative to migration in some flycatchers (Johnson 1963: fig. 1 and references).

Hypotheses to explain these differences are poorly developed; furthermore our basic descriptive data on timing of molts relative to the fall migration are so poor for passerine birds of western North America that attempts at comparative tests of such hypotheses are probably premature. The hypotheses themselves have a curiously negative character implying, without adequate theoretical or empirical justification, that the alter-

TABLE 7. Date, average molt scores, and percentage of specimens growing secondaries or rectrices for subadult male *I. g. galbula* taken while undergoing the first prealternate molt.<sup>a</sup>

|     |       | Number of specimens in molt | Mean molt scores <sup>b</sup> |      |      |        |        | % specimens molting |             |           |
|-----|-------|-----------------------------|-------------------------------|------|------|--------|--------|---------------------|-------------|-----------|
|     |       |                             | Crown                         | Back | Rump | Throat | Breast | Flanks              | Secondaries | Rectrices |
| Sep | 16-30 | 2                           | 0                             | 0    | 0    | 1.0    | 0      | 0                   | 0           | 0         |
| Oct | 1-15  | 3                           | 0                             | 0    | 0    | 1.7    | 0      | 0                   | 0           | 0         |
|     | 16-31 | 1                           | 0                             | 0    | 0    | 2.0    | 0      | 0                   | 0           | 0         |
| Nov | 1-15  | 4                           | 0                             | 0    | 0    | 1.0    | 0      | 0                   | 0           | 0         |
|     | 16-30 | 1                           | 0                             | 0    | 0    | 1.0    | 0      | 0                   | 0           | 0         |
| Dec | 1-15  | 1                           | 0                             | 0    | 0    | 1.0    | 3.0    | 0                   | 0           | 0         |
|     | 16-31 | 3                           | 0.2                           | 0    | 0    | 1.7    | 0      | 0                   | 0           | 0         |
| Jan | 1-15  | 2                           | 0.5                           | 0    | 0    | 3.0    | 1.5    | 0                   | 0           | 0         |
|     | 16-31 | 0                           | —                             | —    | —    | —      | —      | —                   | —           | —         |
| Feb | 1-15  | 4                           | 1.2                           | 0.8  | 0.2  | 1.2    | 1.5    | 0.5                 | 25          | 50        |
|     | 16-29 | 6                           | 1.0                           | 0.2  | 0.7  | 1.7    | 1.5    | 0.3                 | 33          | 50        |
| Mar | 1-15  | 6                           | 1.5                           | 1.3  | 0.6  | 2.8    | 2.0    | 0.5                 | 17          | 50        |
|     | 16-31 | 15                          | 1.7                           | 1.5  | 1.1  | 2.3    | 1.8    | 1.5                 | 53          | 53        |
| Apr | 1-15  | 4                           | 0.8                           | 0.5  | 0.2  | 0.9    | 1.2    | 0                   | 0           | 0         |
|     | 16-30 | 2                           | 1.5                           | 1.5  | 1.5  | 1.5    | 1.5    | 0                   | 50          | 50        |
| May | 1-15  | 3                           | 0.7                           | 0.7  | 0    | 1.0    | 1.3    | 0                   | 100         | 67        |
|     | 16-31 | 4                           | 1.5                           | 0    | 0    | 2.2    | 0.2    | 0                   | 0           | 25        |

<sup>a</sup> Seven April and May specimens, and one October and one January specimen from the United States are included.

<sup>b</sup> Possible range in each body region was 0-3.

native pattern would be better were it achievable. I present two examples, not as criticism of earlier efforts, but with an eye to stimulating further work on the evolutionary ecology of avian molts.

Johnson (1963) argues that the fall molts of *Empidonax hammondi* occur on the breeding grounds, unlike those of *E. wrighti* and *E. oberholseri*, because *E. hammondi* winters at such high elevations that delaying the molts would be impossible. To be complete, this hypothesis requires establishing a benefit to *E. wrighti* and *E. oberholseri* of delaying the fall molts until after the fall migration that is not enjoyed by *E. hammondi* because of its high elevation winter range. Such a benefit has been suggested for the eastern *E. minimus*. In this species both adults and HY birds molt their body feathers on the breeding grounds, but adults delay the molt of their primaries until arrival on the wintering quarters (Hussell 1980, Sealy and Biermann 1983). Sealy and Biermann (1983) argue that adults may delay their primary molt in order to migrate earlier and, thus, benefit from the early establishment of winter territories. This explanation suggests winter territorial species might be more likely to postpone molt until after the fall migration, but no general assessment of the idea has been undertaken.

Rohwer (1971) also constructed a "negative"

hypothesis for certain North American aerial foragers, suggesting that Tree and Violet-green swallows (*Tachycineta bicolor* and *T. thalassina*) and White-throated Swifts (*Aeronautes saxatalis*) molt on their breeding grounds (unlike most other North American members of their families) because the northerly location of their wintering grounds prohibits molting there due to food shortages. The presumed cost of undergoing the prebasic molt on the breeding grounds is their shortened breeding season, resulting in fewer replacement clutches or fewer broods. While this hypothesized advantage of delaying the fall molts until after the migration may be plausible for Barn or Cliff swallows (*Hirundo rustica* and *H. pyrrhonota*) that often or occasionally raise second broods (see Lunk 1962, p. 50), it is unlikely to apply to flycatchers because none of the species that molt after the fall migration (*Tyrannus*; *Empidonax*) raise multiple broods, while some of those that do molt on their breeding grounds (*Sayornis*) are sometimes double brooded (Blancher and Robertson 1982, Johnston 1964: fig. 5).

Two things may be important in explaining the difference in the timing of the molts of *galbula* and *bullockii*. First, most *galbula* from eastern North America probably cross the Gulf of Mexico en route to their winter range in humid

tropical regions of southern Mexico, Central America, and northern South America. This is supported by the occurrence of *galbula* in fall tower kills from Florida and North Carolina (Sealy 1986) and by fall records from Cuba (Bond 1956). Thus, maximum efficiency in the fall flight may be critical to *galbula* but less so to *bullockii* since the latter does not undergo a long overwater passage to reach its wintering grounds in the southwestern United States and western Mexico.

Second, dry late summer conditions characterize most of the breeding range of *bullockii* while rain continues to fall in late summer in the range of *galbula* in eastern North America. Late summer droughts in most of *bullockii*'s range may limit food supplies sufficiently to favor a migration to more productive regions for the fall molts. In fact most *bullockii* seem to undergo just such a migration. Most of the molting specimens, and particularly those taken in heavy molt, were collected either in southern California, Arizona, New Mexico, Sonora, or Chihuahua. This region lies either within or en route to *bullockii*'s winter range, so moving to it in late summer accomplishes much of the fall migration. More importantly, however, this region receives most of its annual precipitation in late summer rainstorms coming from the Gulf of Mexico (Neilson 1986). Indeed these rains peak in July and August (Neilson 1986) and are followed by remarkable flushes of productivity. The effect of these late summer rains is so dramatic that several birds (*Geococcyx californianus*, *Toxostoma curvirostre*, *Aimophila cassini*, and *Pipilo fuscus*) as well as tiger salamanders (*Ambystoma tigrinum*) breed in early spring and again in late summer following these rainstorms (Reichert 1979). We think that *bullockii* departs its drying breeding range and migrates to this region to molt in this flush of productivity. Apparently it is only after this pause for the fall molts that *bullockii* continues on into its principal wintering grounds in the highlands of western Mexico, but more specimens are needed to evaluate this point.

Orchard Orioles (*Icterus spurius*) migrate to Central America before the prebasic molts, adults arriving in El Salvador in "fearfully abraded plumage" and young "still in soft, juvenal feathering" (Dickey and van Rossem 1938). The breeding range of *spurius* largely overlaps that of *galbula* rather than *bullockii*, so it is unclear why it should migrate prior to molting while *galbula* molts before the fall migration. Consistent with

the postponement of the fall molts, *spurius* does not cross the Gulf of Mexico in its fall migration, although it does so in spring. Of the fall migration of *spurius* near Pensacola, Florida, F. M. Weston writes (in Bent 1958): "During 30 years of continuous field observations, I have never under any circumstances of favorable or adverse weather conditions seen any concentrations of orioles, though it is common experience to find thousands of migrants of other species weatherbound on this coast on several occasions every fall."

#### IMPLICATIONS FOR HYBRIDS

The differences between *galbula* and *bullockii* in scheduling and in number of molts (Fig. 1) might create difficulties for hybrids if these differences have any genetic basis. Unfortunately, we excluded late summer specimens from the central Great Plains from this study so the differences in molts in this common environment remain to be evaluated. The following discussion is, thus, necessarily speculative.

The hybrid zone between *bullockii* and *galbula* was first extensively described by Sibley and Short (1964) on the basis of specimens collected in the 1950s. At that time most birds from an approximately 100-km band along the Platte River were of hybrid phenotype. Further field studies and collecting along the Platte River have revealed a high frequency of parental phenotypes and fewer hybrids in more recent years (Edinger 1985, Corbin and Sibley 1977, see also their treatment of data from Rising 1970). Furthermore, Edinger (1985) found pairing to be strongly assortative along the Platte River if the male of the pair was in definitive plumage. At two localities in Montana and Southern Alberta, Rising (1973) found only limited evidence of hybridization between *bullockii* and *galbula*, with pure specimens of both phenotypes predominating in both samples. In contrast, on river systems in central and southern Kansas, Rising (1983a) found no evidence of reduced hybridization in comparisons of samples from the mid-1960s and samples from the late 1970s. In their ensemble these papers suggest the possibility of greater reproductive isolation of *galbula* and *bullockii* in more northern parts of their contact, perhaps because these populations have had a longer history of contact due to the presence of more trees along rivers in the northern plains (see also Rising 1983b).

If, as suggested by Corbin and Sibley (1977) and Edinger (1985), there is selection against hy-

brids, what may be its basis? Differences in plumages and vocalizations (see Edinger 1985 for sonograms) are adequate to serve as prezygotic isolating mechanisms. The problem lies with credible sources of selection against hybrids. Rising (1969) and Corbin and Sibley (1977) suggest differences in ability to thermoregulate and in degree to which individuals aggregate in the nesting season, but *galbula* and *bullockii* are so broadly overlapping in these characteristics that they are only weakly plausible as agents of selection against hybrids.

In contrast, the differences in molt patterns between *galbula* and *bullockii* are striking and without overlap (although they have not yet been documented for Great Plains populations). They differ both in the scheduling of their fall molts relative to the fall migration and in whether or not they have a prealternate molt. Among other possibilities, hybrids (1) might undergo two prebasic molts, prior to and after the fall migration, (2) might delay the migration and molt very late in fall, or (3) might inappropriately either forgo (*galbula*) or attempt (*bullockii*) a prealternate molt. All of these recombinant novelties could seriously jeopardize survival or reproductive success.

Our most interesting specimen with regard to these possibilities is a female collected on 1 November 1971 in Chihuahua (DMNH 13051). Although we assessed this specimen as hybrid before examining it for molt, females are difficult to identify as hybrids. This specimen is in fresh body plumage but in late stages of its primary molt, having P8 growing on each wing (oddly, P5 is also growing on the left wing but this may be due to an accidental loss). What is striking about this specimen is that P9 is fresh on both wings. Since the primaries are molted in ascending numerical sequence and since they also become very worn during the breeding season, P9 would have been noticeably worn had it not been replaced in an earlier molt. The hypothesis that the ninth primaries on this specimen are fresh because the bird is a juvenile may be excluded—the bird had a fully pneumatized skull and it has a black throat which yearling females do not have (Pam Williams, pers. comm.; see also Sealy 1979 and Flood 1984). Assuming this specimen had not accidentally lost both eighth primaries, it appears to be undergoing a second molt of at least its primaries in the same fall. Thus it may have undergone a molt prior to its migration, as would

*galbula*, and have been undergoing a second molt after its migration, as would *bullockii*. Only one other hybrid (USNM 196836): adult male, Beeville, Texas, 18 August 1905; Rising hybrid score = 20) was molting when collected, and it is so far along in the molt (P9 growing; all body plumage new or incoming) that the possibility of a double molt cannot be evaluated. None of the 12 adult males from the wintering grounds, with hybrid scores between 5 and 24 (Rising 1970) was molting, so we cannot further pursue the possibility of hybrids having unusual molts.

#### THEORIES OF SUBADULT PLUMAGES AND THE PREALTERNATE MOLT

The color of feathers grown by subadult males in the prealternate molt is helpful in assessing whether subadult plumages are an adaptation to socioecological conditions of the first breeding season (Rohwer and Butcher 1988). If female-like feathers were grown in the prealternate molt then there would be little doubt that having a female-like plumage was beneficial in the first breeding season. We expected to find such feathers in *bullockii* but were, instead, surprised to find that *bullockii* virtually lacks a prealternate molt. Unfortunately, support for this molt-related prediction is strong only if female-like feathers are grown in the prealternate molt. Female-like feathers retained for the first breeding by *galbula* and *bullockii* may be held because they are adaptive in that season or because, while adult-male-like feathers would be more advantageous, there is some constraint on molting in spring (Rohwer and Butcher 1988).

Three points about *galbula*'s prealternate molt suggest that the subadult plumage of this form is better viewed as an adaptation to the first winter rather than to the first breeding season. First there is a prealternate molt which, in some few subadults, is so extensive that they closely resemble adult males in body coloration for their first breeding season. Second, almost every growing feather on 28 of 29 subadults taken in the prealternate molt was entirely adult-male-like; assuming the odd specimen growing female-like feathers was missexed, the spring molt always serves to remove female-like feathers. And third, the fact that the molt is either continued or resumed by some subadults after their arrival on the breeding grounds further suggests that female-like feathers may be undesirable in the breeding season.

Conflicting with these points, however, is the fact that the pairing success of subadult *galbula* seems unaffected by their appearance. Flood (1984) found duller, more female-like subadults to be as likely to breed as more conspicuous subadults. A similar lack of correlation between subadult coloration and mating success has been found for Purple Martins, *Progne subis* (Rohwer and Niles 1979). However, for Indigo Buntings, *Passerina cyanea* (Payne 1982), and Corn Buntings, *Emberiza calandra* (Möller, unpubl.), positive correlations have been found between the pairing success of first-year males and the possession of a more adult-male-like subadult plumage.

Since *bullockii* subadults do not undergo a prenuptial molt, the female-like plumage of young males may be viewed, with equal plausibility, either as an adaptation to their first winter or to their first breeding season.

#### WINTER STATUS SIGNALING AND MOLT PATTERNS

The most plausible explanation for adult passerines being more conspicuous than immatures in winter is the winter status signaling hypothesis (Rohwer and Butcher 1988). Both young and adult passerines always undergo a complete molt of body feathers in the fall. For species in which both age classes also undergo complete molts of their body plumage in the spring, we know the winter plumage is unconstrained by signaling requirements of the breeding season. But for species that lack a prealternate molt or that have an incomplete prealternate molt of body feathers, it is more difficult to determine whether or not differences in the appearance of the age and sex classes are adaptive in winter. This is the case for *bullockii* and for female and adult male *galbula* but less so for subadult male *galbula* in which the prealternate molt of body feathers is, in many individuals, fairly extensive.

Here we consider features of the spring and autumnal molts and the plumages they produce that are and are not interpretable under the winter status signaling hypothesis. The conspicuous plumage of adult male *bullockii* and *galbula* may be functional either in winter or in summer or in both seasons. This follows from the lack of independence of the winter and summer appearance of adults due to the absence of a prealternate molt in *bullockii* and its extremely re-

stricted nature in *galbula*. One point, however, suggests that a conspicuous plumage in winter is important to adult males. Their fresh fall feathers are not extensively veiled by cryptic tips; some individuals exhibit no veiling at all while others have limited buffy tips on the ends of the black feathers of the back. Cryptic tipping is considerably more extensive in some icterids (e.g., Red-winged Blackbird; Rusty Blackbird, *Euphagus carolinus*) and is an avenue to the development of substantial independence of the fall and spring appearance when molting in spring is constrained.

The temporal pattern of development of the black throat patch in subadult male *galbula* is particularly suggestive of winter status signaling. In *bullockii* (and also *abeillei* as shown by specimens in the Moore collection) young males acquire the black throat in the first prebasic molt which occurs in August or September. In *galbula*, however, young males do not acquire a black throat in the first prebasic molt, but initiate a second, low-intensity molt of their throat feathers soon after the fall migration. This feather replacement is not a completion of the first prebasic molt (known because of the texture difference between the juvenile and first fall plumage) but an extreme seasonal advancement of the prealternate molt. Its effect is that many young males acquire considerable amounts of black in their throats by late January and, thus, become distinguishable from all young females (see Flood 1984 on female plumage change with age) and some adult females. This early acquisition of the black throat by *galbula* subadult males seems most plausibly attributed to benefits of winter status signaling because it serves to distinguish them from all yearling females. Young males presumably are socially dominant to young females and, thus, may benefit from early acquisition of a distinctive badge to advertise their status.

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