

FIRST-YEAR PLUMAGES OF THE BROWN-HEADED COWBIRD AND REDWINGED BLACKBIRD

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The postjuvinal molt in the Brown-headed Cowbird (*Molothrus ater*) and the Red-winged Blackbird (*Agelaius phoeniceus*) has often been reported to involve complete replacement of juvenal feathers, producing, in male and female *Molothrus* and female *Agelaius*, first-year plumages which are indistinguishable from adult plumages (Dwight, 1900; see also Friedmann, 1929:280–283, and Bent, 1958). It was recently noted (Selander, 1958), however, that a basis for age determination in these and some other related icterids is provided by the fact that some juvenal feathers, especially under wing coverts and tertiaries, may be retained through the postjuvinal molt. And Baird (1958), working independently in Rhode Island, also found that the postjuvinal molt in male *Molothrus ater* is normally incomplete.

In the present study, first-year plumages of *Molothrus ater* and *Agelaius phoeniceus* are considered in detail, and some data on retention of juvenal feathers in the Brewer Blackbird (*Euphagus cyanocephalus*) and the Common Grackle (*Quiscalus quiscula*) are also presented. We have been concerned primarily with four questions: (1) What percentages of juveniles of these species have an incomplete postjuvinal molt? (2) What is the extent of intra- and inter-specific variation in types and numbers of juvenal feathers retained by first-year birds? (3) Is there evidence of correlation in first-year birds between numbers of feathers retained and age at molt? (4) What, if any, is the adaptive significance of individual variation in extent of the postjuvinal molt in icterids?

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MATERIALS AND METHODS

This study is based on specimens collected from flocks wintering in southern Texas in 1958, as follows—*Molothrus ater*: Colorado County, November 8, 39 specimens; Frio County, November 22, 42 specimens, November 29, 47 specimens. *Agelaius phoeniceus*: Frio County, November 29, 78 specimens. *Euphagus cyanocephalus*: Frio County, November 22 and 29, 14 specimens. *Quiscalus quiscula*: Colorado County, November 8, 2 specimens; Frio County, November 29, 4 specimens.

Our specimens of *Molothrus ater* are, as a group, intermediate in size between "typical" *M. a. ater* and *M. a. obscurus*. Those from Colorado County, in southeastern Texas, average slightly larger than those from Frio County, 170 miles to the southwest. Both counties lie within a broad zone of intergradation between breeding populations of *M. a. ater* and *M. a. obscurus* which extends over much of central Texas (A.O.U. Check-list, 1957:540–542, and Friedmann, 1929:fig. 6, p. 146). It is likely that flocks wintering in these areas are composed largely of resident birds, but these may be joined by wintering individuals of *M. a. ater* from the eastern United States.

Specimens of *Agelaius phoeniceus* were not identified racially, but it is probable that the majority represented *A. p. megapotamus*, which is resident in central southern Texas. The Common Grackles examined in this study are referable to *Q. q. versicolor*.

CRANIAL OSSIFICATION

In all species studied it may reasonably be assumed that the cranium becomes completely ossified before the end of the first year of life. Hence, specimens showing incomplete ossification were judged to be first-year birds. Most of our specimens with completely ossified skulls are doubtless adult (more than one year in age), but a small

percentage may represent precocious first-year individuals in which complete development was achieved relatively early. Specimens were assigned to one of six progressive stages of cranial development defined as follows:

STAGE	DESCRIPTION
1	Ossification (double-layered condition) evident only in occipital region and in narrow band along mid-line.
2	Ossification present in wide band along mid-line and over most of posterior part of cranium.
3	Approximately one-half of area of cranium ossified.
4	Approximately three-quarters of area of cranium ossified.
5	Cranium ossified except for small patches about 3 mm. in diameter on either side.
6	Cranium completely ossified.

PTERYLOGRAPHY

The pterylography of the under wing in the genera studied is similar to that previously described for the Great-tailed Grackle, *Cassidix mexicanus* (Selander, 1958: 355-357), with two minor exceptions. In *Cassidix* there are series of 10 under greater, middle, and lesser secondary coverts. But in *Molothrus*, *Agelaius*, and *Euphagus* (and also, incidentally, *Tangavius* and *Sturnella*), only 9 greater secondary and 9 middle secondary coverts are present, and the series of lesser secondary coverts is incomplete; those lesser secondary coverts present are greatly reduced in size, and in some cases they are vestigial. An intermediate condition is seen in *Quiscalus*, in which there are 10 greater secondary coverts but only 9 middle secondary coverts; lesser secondary coverts are not well developed in *Quiscalus*. In all these genera there are series of 9 under greater and middle primary coverts and two carpal remex coverts; under lesser primary coverts are not represented.

Juvenal feather types commonly retained by first-year birds are under greater and middle primary and secondary coverts, carpal remex coverts, long coverts on the ventral surface of the patagial membrane, and tertiaries. In exceptional cases, juvenal feathers of other types may also be retained.

MOLOTHRUS ATER

In a sample of 67 specimens of *Molothrus ater*, cranial ossification was incomplete in 49 and complete in 18. All members of the latter group had completely replaced the plumage at the fall molt, but 48 of the 49 birds with incompletely ossified skulls had retained some juvenal feathers (fig. 1). The exceptional individual, a male, had an unossified area 3 mm. in diameter on the left side of the cranium. Possibly this bird was an adult in which skull development was abnormally delayed, but it is much more probable that it was a first-year individual which had experienced a complete postjuvenal molt. Evidence that the skull in first-year birds is occasionally almost, if not fully, ossified by November is provided by another male, whose age is indicated by the fact that it had retained six juvenal under greater primary coverts. The skull of this bird was completely ossified except for a single area 3 mm. in diameter on either side of the cranium (stage 5).

Percentages of first-year birds retaining various types of juvenal feathers are given for *Molothrus ater* and *Agelaius phoeniceus* in table 1. Mean numbers of various feather types retained by these species are shown in table 2. Histograms showing percentages of males retaining different numbers of various types of juvenal feathers are presented in figure 2.

The foregoing data clearly indicate that the postjuvenal molt in *Molothrus ater* is

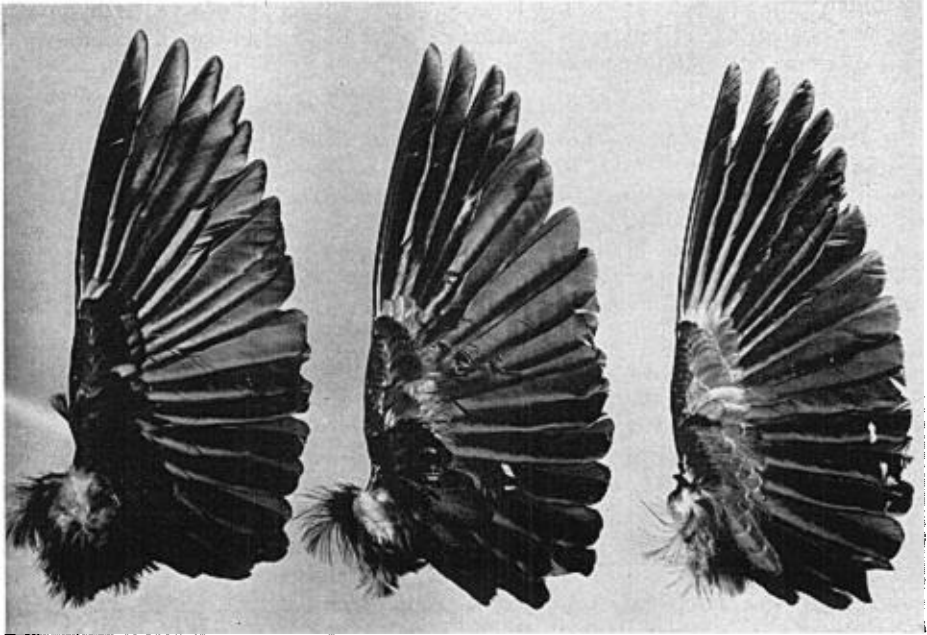


Fig. 1. Ventral view of wings of male *Molothrus ater*. Left, an adult male; center, a first-year male showing partial retention of juvenal wing coverts; right, a first-year male which had retained most of the juvenal under wing coverts. New feathers grown at the fall molt are glossy black; juvenal feathers are dull brown.

normally incomplete. Apparently only about 2 per cent of juveniles have a complete molt. Baird (1958:225) did not determine the cranial conditions of individuals of *M. a. ater* which he examined, and, thus, he was unable to determine the percentage of juveniles completing the postjuvenal molt; but he was correct in believing that it is very small. Compared with *Agelaius phoeniceus* and *Cassidix mexicanus*, a smaller percentage of juveniles of *Molothrus ater* undergo complete postjuvenal molt, a greater percentage of first-year birds retain juvenal wing coverts, and average numbers of feathers retained are greater.

In males of *Molothrus ater*, recognition of retained juvenal feathers is a simple matter, for they are dull brown, whereas new feathers grown in the postjuvenal molt are glossy black (fig. 1). Even males in worn breeding plumage may readily be aged by this method. In females, on the other hand, the similarity in color of retained juvenal feathers and new feathers of the first-winter plumage "renders detection of vestiges of the juvenal plumage exceedingly difficult" (Baird, 1958:226). Working with specimens in fresh fall plumage, we were able to identify retained juvenal feathers by noting subtle differences in size, shape, color, and degree of wear; but these differences become increasingly less apparent with wear of the plumage, and we have had little success in aging females taken later than March.

In males having incomplete postjuvenal molt, the total number of retained under wing coverts and tertiaries varies from 2 to 55, with an average of 27.2. Females apparently retain fewer feathers than males, but larger samples of females would be necessary to substantiate this point. It is noteworthy that none of our females retained patagial coverts, whereas 42 per cent of males retained one or more of these feathers.

Table 1

Percentages of First-year Birds Retaining Juvenal Feathers of Various Types

Species and sex	Number	Under greater primary coverts	Under greater secondary coverts	Under middle primary coverts	Under middle secondary coverts	Patagials	Tertiaries	Estimated per cent of birds having complete post-juvenal molt
<i>Molothrus</i>								
<i>ater</i>								
Male	39	97	92	66	37	42	82	2
Female	10	100	100	80	50	0	70	?
<i>Agelaius</i>								
<i>phoeniceus</i>								
Male	64	77	70	20	11	16	80	16
Female	47	28
<i>Cassidix</i>								
<i>mexicanus</i> ¹								
Male	77	90	65	78	8
Female	55	84	74	85	12
<i>Euphagus</i>								
<i>cyanocephalus</i>								
Male	8	100	100	100	37	0	88	?
<i>Quiscalus</i>								
<i>quiscula</i>								
Male	2	100	100	0	0	50	100	?
Female	2	100	100	50	50	100	100	?

¹ Data from Selander (1958).

Normally, only under primary and secondary coverts, long patagial coverts, and tertiaries are retained, but other types of juvenal feathers are also present in seven males in our series. In addition to a total of 55 under wing coverts and tertiaries, one male retained the following feathers: 6 small marginal coverts of the leading edge of the patagium, 1 marginal covert on the manus, 16 breast feathers, about half the thigh feathers, many small marginal coverts adjacent to the anterior part of the humeral tract (epaulet coverts), and several feathers laterally on the cervical and dorsal regions of the spinal tract. A second bird with a total of 41 juvenal coverts and tertiaries also retained 10 small marginal coverts of the patagium. A third male showed 53 retained feathers of the usual types, together with many epaulet coverts, one breast feather, and primary 5 in the right wing. A fourth specimen retained 54 under wing coverts and tertiaries, in addition to 2 small marginal coverts of the patagium and 6 epaulet coverts. A fifth male showed 53 retained coverts and tertiaries, in addition to 5 epaulet coverts, 5 breast feathers, a few flank feathers, and several feathers of the cervical region. Two other males, both of which had retained 53 coverts and tertiaries, had failed to molt some juvenal feathers at the edges of the spinal tract. We found no comparable irregularities in females. Similarly, retention of unusual types and numbers of juvenal feathers in *Cassidix mexicanus* is much more frequent in first-year males than in females (Selander, 1958:363).

Comparison of Baird's data (1958) for Rhode Island with ours from south-central Texas suggests geographic variation in percentages of males retaining juvenal feathers of certain types, with birds from the north more frequently retaining feathers. In a sample of unspecified size, Baird found juvenal feathers along the mid-line of the belly in 23 per cent of first-year males, whereas this condition occurred in only 8 per cent of our sample of 39 males. Twenty-three per cent of Rhode Island males versus 11 per cent

in our sample had retained some feathers of the spinal tract. Baird noted that 92 per cent of his birds failed to molt the last two feathers of the scapulars (humeral tract). The feathers to which he refers are herein called tertiaries, following Miller's terminology (1928:396); they are inserted along the posterior edge of the humerus and are concealed by the adjacent scapulars. Eighty-two per cent of our males retained one or more of these feathers. In 9 per cent of Baird's males, molt of the orbital region had been incomplete, but this condition was not found in our series.

Table 2

Species and sex	Number	Mean Numbers of Juvenal Feathers Retained by First-year Birds				Patagials	Tertiaries	Totals
		Under greater primary coverts	Under greater secondary coverts	Under middle primary coverts	Under middle secondary coverts			
<i>Molothrus ater</i>								
Male	39	7.7	7.3	3.2	2.6	2.5	3.9	27.2
Female	10	7.3	6.7	2.8	2.0	0.0	1.9	20.7
<i>Agelaius phoeniceus</i>								
Male	64	4.6	5.0	0.5	0.3	0.9	3.2	14.5
<i>Cassidix mexicanus</i> ¹								
Male	77	4.3
Female	55	4.0
<i>Euphagus cyanocephalus</i>								
Male	8	8.9	7.6	4.7	1.7	0.0	2.2	25.1
Female	1	9	9	3	2	0	0	23
<i>Quiscalus quiscula</i>								
Male	2	7.5	6.0	0.0	0.0	3.5	5.0	22.0
Female	2	8.0	8.0	0.5	1.0	5.0	4.5	27.0

¹ Data from Selander (1958).

Dwight (1900:159) mentions one specimen of *Molothrus ater* "which retains a large part of the juvenal plumage even to the wing quills . . ." In the Shiny Cowbird (*Molothrus bonariensis*) of South America, apparently even greater numbers of juvenal feathers are retained by first-year birds than in *Molothrus ater*. Friedmann (1929:134) notes that first-year males "usually retain some of the brown wing or tail feathers and sometimes some of the juvenal body feathers as well. In this species . . . about 80 per cent of the birds retain at least one or two juvenal wing or tail feathers . . ."

Correlations.—When comparisons are made between stage of cranial ossification and total number of retained under wing coverts and tertiaries, an inverse relation is apparent (fig. 3). Since degree of advancement of skull development is to some extent a function of age, we infer that birds hatched early in the breeding season tend to retain fewer juvenal feathers through the postjuvenal molt than do those hatched later in the season.

It is perhaps surprising that no correlation exists between numbers of retained juvenal feathers and weight or linear measurements (fig. 3). Even those individuals in which retention is most marked are not smaller or lighter in weight than the average run of specimens. Similarly, in another icterid, *Cassidix mexicanus*, only one of eight birds showing retention of unusual types of juvenal feathers was abnormally light in

weight (Selander, 1958:365). This contrasts with the situation in the Loggerhead Shrike (*Lanius ludovicianus*), in which first-year birds retaining unusually large numbers of juvenal feathers are often "runts" (Miller, 1931:27).

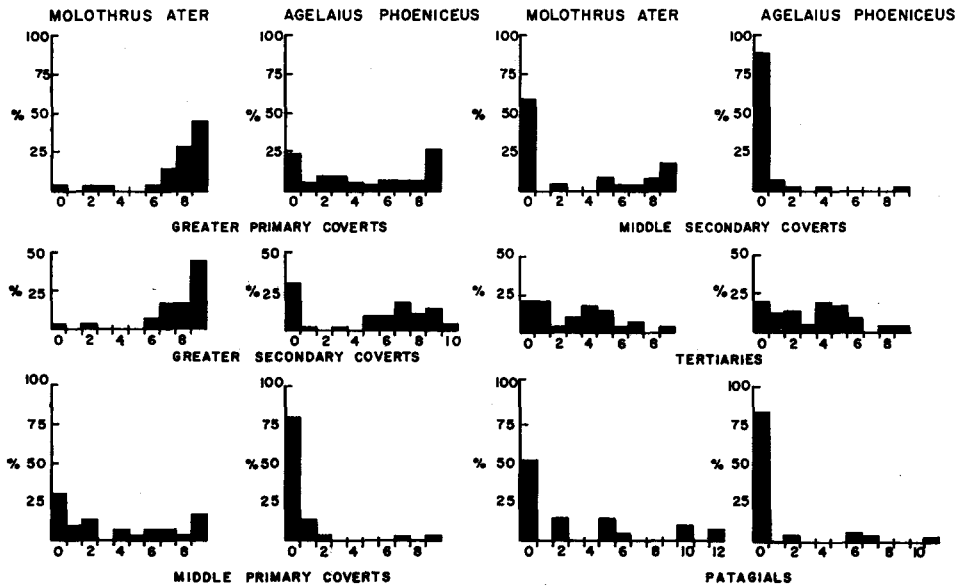


Fig. 2. Individual variation in numbers of juvenal under wing coverts and tertiaries retained through the postjuvinal molt by males of *Molothrus ater* and *Agelaius phoeniceus*. The histograms show percentages of males retaining indicated numbers of feathers. All specimens were taken in October.

Color differences between adult and first-year plumages.—Ignoring the presence of juvenal feathers in plumages of first-year birds, our first-year and adult specimens are almost identical in color. Adult males average slightly darker and more glossy than first-year birds, but the difference is too inconstant to be of real value in age determination. Baird (1958:226) noted that the head is less conspicuously tinged with purple in adults than in first-years, a distinction which is also apparent in our material. To test this character, we paired first-year and adult male specimens at random and compared the members of each pair. In 60 per cent of the pairs, purple was more conspicuous in the first-year bird; in 30 per cent there was no difference between the specimens; and in 10 per cent purple was more conspicuous in the adult bird.

Compared with first-year females, adult females are generally darker, are less mottled dorsally, show less conspicuous striping ventrally, and tend to have the light brown edgings of the remiges less conspicuous because they are darker and contrast less with other parts of these feathers. But, again, these are only average differences and there is much overlap between the two age groups.

Size differences between age groups.—Wing and tail average shorter in first-year males than in adult males, but there are no significant age differences in bill length, bill depth, tarsus length, or weight. Wing and tail measurements (in millimeters) of 20 adult males averaged 106.7 ± 0.7 and 75.6 ± 0.5 ; comparable mean measurements of 29 first-year males were 104.5 ± 0.4 and 73.3 ± 0.4 . There are no significant age differences in size in females.

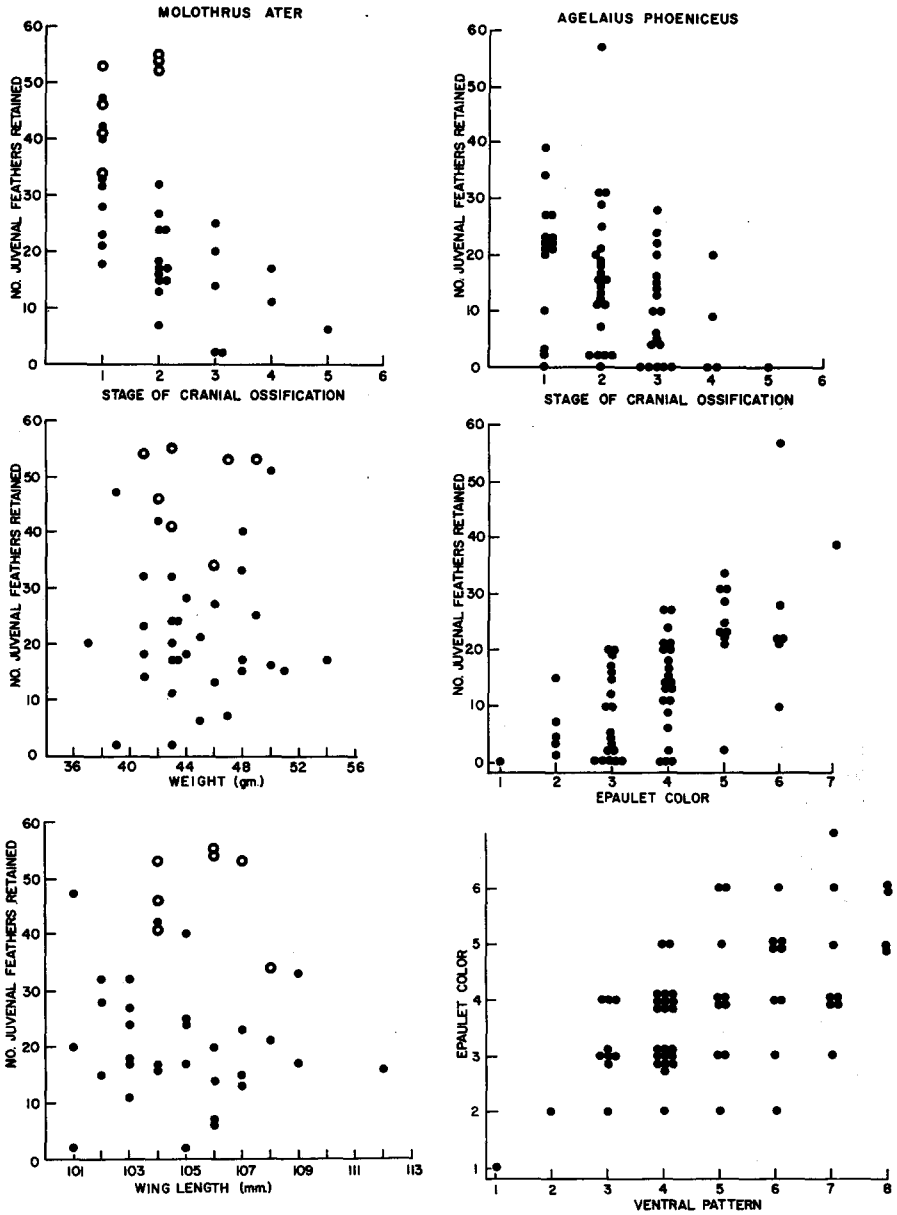


Fig. 3. Correlation graphs (see text for explanation). The open symbols represent first-year individuals of *Molothrus ater* which had retained unusually large numbers of juvenile feathers.

AGELAIUS PHOENICEUS

MALES

In a series of 71 male specimens, seven had completely ossified skulls and were judged to be adult; all seven were in completely new plumage. Of the 64 first-year birds, 10 were in completely new plumage and 54 showed some retained juvenile feathers. It would seem, therefore, that about 16 per cent of juvenile males have a complete post-

juvenile molt. Percentages of first-year birds retaining juvenal feathers of various types and mean numbers retained are shown in tables 1 and 2.

The male juvenal plumage of this species is similar in color and pattern to that of the adult or first-year female. At the postjuvenal molt, the degree to which the new feathers of the first-year plumage depart from the juvenal pattern and approach or resemble the adult male plumage varies tremendously (see fig. 4), as noted by Ridgway (1902), Allen (1914), Wright and Wright (1944), and others. The resulting first-year plumage is, on the average, one in which, as described by Dwight (1900:160), the "entire plumage, including wings and tail, [is] greenish black much veiled with buffy and ferruginous edgings, palest below and faint or absent on primaries and rectrices. Lesser wing coverts ('shoulders') dull orpiment-orange each feather with subterminal bars or spots of black. Median coverts rich ochraceous buff usually mottled with black subterminal areas chiefly on the inner webs, the shafts usually black." The adult male plumage is described by Dwight (*loc. cit.*) as follows: "Lustrous greenish black, feathers of head and back, greater wing coverts and tertiaries edged more or less (according to the individual) with buff and ferruginous brown. Below, the edgings are paler or absent. The bright scarlet-vermilion 'shoulders' are acquired together with the rich ochraceous buff median coverts."

To analyze variation in pattern, we selected a series of eight specimens representing categories in the span of variation in pattern of the under parts, which area provides a good index to patterning of the plumage generally (fig. 4). Specimen 1 was an adult that completely lacked the buff or brown feather edgings mentioned by Dwight; specimen 8, a first-year bird, was among the most heavily mottled birds available; and specimens 2

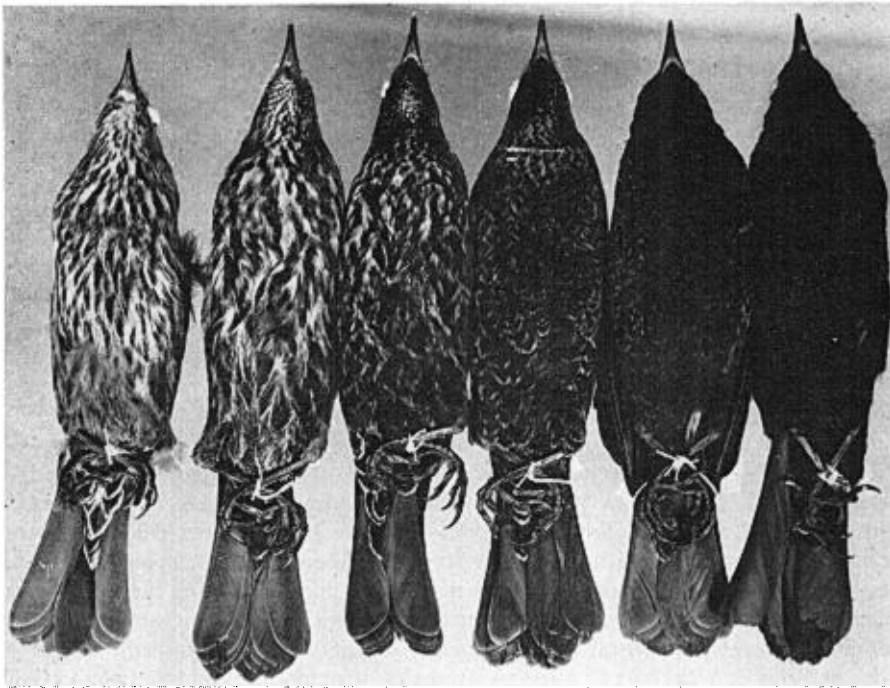


Fig. 4. Specimens of *Agelaius phoeniceus* in ventral view. From left to right: an adult female, four first-year males showing variation in first-year plumage, and an adult male.

to 7 were to various degrees intermediate between these extremes. Seven categories of epaulet color were also established, ranging from intense red (category 1) through orange to yellow (category 7) and covering the span of variation shown by our series. Each specimen was then compared with the reference series and assigned to appropriate categories of patterning of the under parts and of epaulet color. The resulting data are shown in figure 5. Especially impressive is the wide range of variation exhibited by first-year birds. Most first-year specimens are easily distinguished from adults, but adult and first-year males overlap to some extent in both characters.

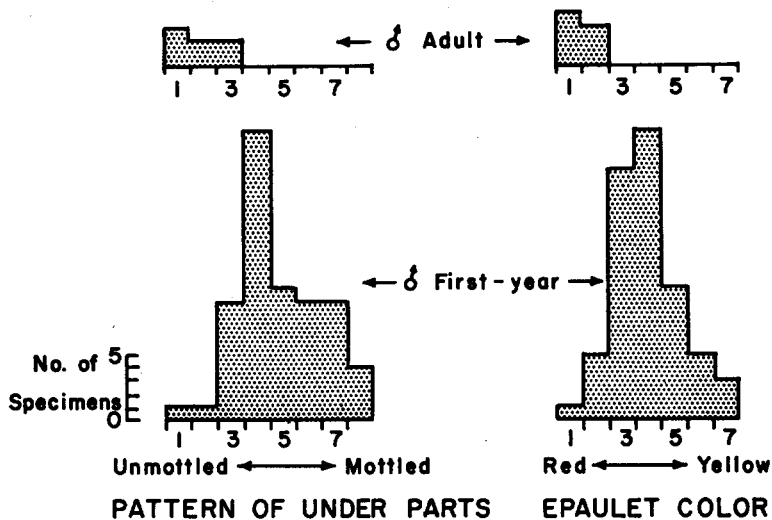


Fig. 5. Individual and age variation in pattern of the under parts and in epaulet color in adult and first-year male *Agelaius phoeniceus*.

Studying male plumages as background for investigation of the testis cycle of *Agelaius phoeniceus* in Montana and Wisconsin, Wright and Wright (1944:48) found that about three per cent of birds classified as first-year "had plumages very nearly like those of adults." That at least one of these was, in fact, first-year was demonstrated by the presence of a well developed bursa of Fabricius, a structure absent in adults. Using the bursa technique, Wright and Wright were able to show that other "adult-appearing" subadult birds were actually year-olds rather than two-year-olds, as had been suggested earlier by Allen (1914), who may have been influenced by Ridgway's comments (1902). Our data support the findings of Wright and Wright.

Correlations.—In this species there is a correlation between epaulet color and ventral pattern (fig. 3); birds having adult or adult-like body plumage (with little or no brown edging) also tend to have bright red epaulets. Both epaulet color and ventral pattern are also correlated with number of juvenal feathers retained; epaulet color tends to be yellow, and the under parts heavily mottled, in birds retaining large numbers of feathers. As in *Molothrus ater*, there is an inverse relation in first-year birds between stage of skull development and total number of juvenal feathers retained.

Size differences between age groups.—In males, wing and tail length average shorter in first-year than in adult specimens. Mean wing length in 54 first-year birds was 113.7 mm. (range, 108–121) versus 118.0 mm. (range, 117–119) in seven adults. In other

linear dimensions and in weight, the two age groups did not differ; and we found no significant size differences between first-year and adult females.

FEMALES

In our series of 59 females, 45 had incompletely ossified skulls and were first-year. Of the remaining 14, 12 were adult, and two appeared to be first-year birds in which complete ossification had occurred, for each showed some juvenal tertiaries. Our series thus included at least 47 first-year birds; of these, 13 (or 28 per cent) failed to retain any juvenal feathers through the postjuvenal molt. Percentages of females retaining various types of feathers and the numbers of feathers retained were not recorded; we noted only the presence or absence of juvenal feathers.

In females of *Agelaius*, as in those of *Molothrus*, it is difficult to identify juvenal feathers in first-year plumages, for they may differ from new feathers only slightly in color, shape, and size. In males of *Agelaius*, however, a distinction is easily made at all seasons between the brown juvenal feathers and the black feathers grown in the post-juvenal molt.

First-year female plumages invariably resemble the adult female plumage and show comparatively little individual variation in pattern. The most variable feature of the first-year plumage is the hue and distribution of epaulet color. To test Dwight's (1900: 161) supposition that there is a relation between age and amount of orange or red on

Table 3

Individual and Age Variation in Epaulet Color in Female *Agelaius phoeniceus*

Age group	Number of specimens	1	2-Y	2-O	Epaulet categories		3-R	4-R
					2-R	3-O		
First-year	47	20	8	5	3	2	7	2
Adult	12				1		6	5

the epaulets, we have analyzed and compared variation in color in 47 first-year and 12 adult females by assigning each specimen to one of a series of categories (table 3). Birds in category 1 show no bright pigment on the epaulets; those in category 2 have the epaulets faintly tinged with yellow, orange, or red (2-Y, 2-O, 2-R); in category 3, pigments are either orange or red (3-O, 3-R) and form a patch covering approximately one-half the total epaulet area; and in category 4, most of the epaulet area is brightly colored and the hue is invariably red. Most first-year females fall in categories 1 and 2, whereas all but one of our 12 adults were assigned to categories 3-R and 4-R.

Nero (1954:140) has suggested that females in first-year plumage show less pink or salmon tinge about the head and chin than do adults. We have not analyzed variation in this character, but an average difference was noted in processing our specimens.

NOTES ON OTHER ICTERIDS

Euphagus cyanocephalus.—Our series of nine males of this species taken in November consisted of one adult and eight first-year birds, as indicated by the skull character. The first-year birds are in cranial stages 1 to 4. The adult was in completely new plumage, but all first-year birds showed retained juvenal under wing coverts and tertiaries (see table 1). Two first-year females were examined, both of which showed retained juvenal feathers. The data for this species, although limited, suggest that the post-juvenal molt is usually, if not invariably, incomplete. Approximately equal numbers of feathers are retained in *Euphagus cyanocephalus*, *Molothrus ater*, and *Quiscalus quiscula* (table 2).

It is generally believed that first-year males of *Euphagus cyanocephalus* may be distinguished from adults by the presence of narrow grayish brown tips on the feathers of the body plumage (Ridgway, 1902:248-249). All our first-year males show this character to some degree, but its expression is highly variable. In two specimens the light tipping is confined to a few feathers on the head, and it would not be surprising to find, in a larger series, some first-year specimens which lack this character altogether.

Quiscalus quiscula.—Four of our six November-taken specimens were first-year birds that showed unossified cranial areas and retained juvenal feathers (tables 1 and 2). Whether or not the postjuvenal molt is ever complete in this species remains to be determined by larger sampling.

DISCUSSION

It has been noted by Baird (1958) that the types of juvenal feathers normally retained in first-year plumages in *Molothrus ater* are those which would be replaced relatively late in a complete molt. The same holds true for *Cassidix mexicanus* (Selander, 1958) and, presumably, for other icterid genera as well. In the postnuptial molt in *Cassidix*, the under middle wing coverts are lost, more or less as a unit, about midway through the molt, as primary 5 is dropped; and the under greater coverts and long patagial coverts are not replaced until primary 7 is three-quarters grown, when they are molted almost simultaneously. It has also been found in *Cassidix* that full development of the under wing coverts and tertiaries of the juvenal plumage is delayed until after fledging, a condition which may also be characteristic of other icterids if not of passerines in general. Therefore, it is likely that the postjuvenal molt of some late-hatching individuals begins only a few days after, if not before, these late-developing feathers have completed their growth. In such birds, these feathers are fresh at the time of postjuvenal molt; and, because of their protected position under the wing, they will be subject to only a minimal amount of wear before they are renewed in the first postnuptial (second fall) molt. For these reasons, there is probably an advantage, from the standpoint of conserving metabolic energy, in not replacing them in the postjuvenal molt. Moreover, it would seem that the physiologic mechanism controlling molt of these feather types is so adjusted that early-hatching birds, in which these feathers are worn for several weeks or months prior to postjuvenal molt, tend to replace more of them than do individuals hatched later in the season. This mechanism would reduce possibilities of feathers becoming dangerously worn before being replaced in the postnuptial molt.

In considering the adaptive significance of partial postjuvenal molts, attention should be called to an early paper by Miller (1928:414) on *Lanius ludovicianus*, in which it is suggested that "replacements [of juvenal feathers] constitute an adaptation for the purpose of reinforcing the most vulnerable parts of the plumage." The idea that retention of well protected juvenal feathers has adaptive significance in metabolic terms is implicit in Miller's discussion.

Our data suggest that the degree to which the first-year plumage of males of *Agelaius phoeniceus* approaches the adult plumage in pattern and color depends, at least in part, on the age of the individual juvenile at the time of molt. Presumably the underlying physiologic mechanism, which is probably distinct from that influencing degree of feather replacement, involves hormonal modification of the feather follicles or a progressive maturation of the follicles themselves independent of hormonal influence. The great variability of first-year plumages recalls a comparable condition in the Phainopepla (*Phainopepla nitens*), studied by Miller (1933), in which it has been suggested that variable deposition of melanin pigment in males in postjuvenal molt is due to vari-

able levels of testicular hormone at the time of molt. In the present case, however, we doubt that testosterone is a factor modifying feather color and pattern, although we have, as yet, no experimental evidence on *Agelaius* to support our view. Basis for our doubt is the fact that in the related icterid genus *Cassidix*, in which, as in *Agelaius*, first-year male plumages are highly variable and tend to be intermediate between juvenal and adult plumages, implantation of testosterone pellets in 10-day-old nestlings failed to affect color or pattern of either the juvenal or first-year plumages of males or females (Selander, MS). We suspect that color and pattern of plumages of *Agelaius phoeniceus*, and of other related icterids, may similarly be independent of the influence of this hormone.

It is worth emphasizing again that not all juveniles of *Molothrus ater*, *Agelaius phoeniceus*, and *Cassidix mexicanus* have an incomplete postjuvenal molt; and further studies of *Euphagus* and *Quiscalus* may show that at least small percentages of juveniles of these genera also undergo complete postjuvenal molt. Hence, the presence of retained juvenal feathers following the fall molt is clearly indicative of first-year age, but birds lacking such feathers may be either adult or first-year. In our material, the proportion of juveniles in which postjuvenal molt was complete ranged from 2 per cent in male *Molothrus ater* to 28 per cent in female *Agelaius phoeniceus*; and it is likely that some geographic variation in this regard will be found in all species.

SUMMARY

This study has dealt in large part with retention of juvenal feathers by first-year Brown-headed Cowbirds (*Molothrus ater*), Redwinged Blackbirds (*Agelaius phoeniceus*), and some related icterid genera. The proportion of juveniles having complete postjuvenal molt ranges from 2 per cent in male *Molothrus ater* to 28 per cent in female *Agelaius phoeniceus*. Juvenal feather types commonly retained are under greater and middle primary and secondary coverts, under carpal remex coverts, long coverts of the ventral surface of the patagium, and tertiaries. The presence of juvenal feathers in first-year plumages provides a useful, but not absolute, criterion for age determination.

In *Molothrus ater* and *Agelaius phoeniceus*, it is demonstrated that the total number of retained juvenal feathers is inversely related to age at time of postjuvenal molt, as indicated by degree of cranial ossification. In first-year males of the latter species, general plumage pattern and epaulet color are also related to age at time of molt; and, in females of this species, there is a significant average difference in epaulet color between first-year birds and adults.

It is suggested that there is an advantage, from the standpoint of conserving metabolic energy, in not replacing certain late-developing and well-protected feathers of the juvenal plumage. The physiologic mechanism controlling molt of these feather types appears to be so adjusted that early-hatching individuals tend to replace more of them than do birds hatched later in the season, thus reducing possibilities of feathers becoming excessively worn before they are replaced in the postnuptial molt.

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