ADDITIONAL NOTES ON THE PLUMAGE OF THE REDWINGED BLACKBIRD

ROBERT W. NERO

INTRODUCTION

In a previous report on plumage aberrations in the Redwinged Blackbird (Agelaius phoeniceus), I (1954) pointed out the high frequency of occurrence of certain albinotic traits in this species. The results of a detailed examination of a random sample of more than 200 adult males that were collected near Madison, Wisconsin, were particularly interesting. Recently, I have been able to make a similar analysis of a large sample collected near Regina, Saskatchewan, the results of which are reported below. In addition, an analysis of variable black patterns of the middle coverts of the wing and brief experiments on the red pigmentation of the wing coverts are described.

FREQUENCY OF OCCURRENCE OF ALBINOTIC TRAITS IN ANOTHER SAMPLE OF REDWINGS

One hundred territorial adult male Redwinged Blackbirds were collected within 60 miles of Regina between 14 May and 12 July 1956. Examination of this sample for albinotic plumage aberrations showed a close similarity with results obtained in a previous study (Nero, *op. cit.*) of 219 collected near Madison, Wisconsin (see Table 1).

TABLE 1

Trait	Per cent Regina	Per cent Madison
"'Red Spotting'"	34	27
"Breast Banding"	15	11
"Metacarpal Red"	21	20
"White Belly-spot"	19	23
"White Tail-base"	90	88

FREQUENCY OF OCCURRENCE OF FIVE ABERRANT PLUMAGE TRAITS IN Adult Male Redwinged Blackbirds from Two Localities

A comparison of the range of variability of a single one of these traits—"white tail-base" (depigmentation of the base of the tail feathers)—between the Madison and Regina samples is shown in Table 2.

TABLE 2

Extent (maximum length of white area in mm.)	Per cent Regina (100 birds)	Per cent Madison (127 birds)
1–5	7	11
6-10	22	29
11-15	37	42
16-20	20	12
21–25	4	2
25 (and over)	0	4

COMPARISON OF THE RANGE OF VARIABILITY OF A SINCLE Albinotic Trait—"White Tail-base"

The similarity of occurrence of all of these traits in two widely separated populations suggests that in the Redwinged Blackbird these plumage aberrations are characteristic of the species. The evolutionary significance of specific albinotic traits, particularly "breast banding," which is sometimes visible in the field, is not clear.

The Variability of Black Pigment Patterns in the Middle Coverts of the Wing

According to Baird, Brewer, and Ridgway (1905: 160), "The middle coverts are usually uniform brownish-yellow to the very tips; sometimes some of these middle coverts are tipped at the end with black, but these black tips are usually of slight extent, and indicate immaturity, or else a transition of hybridism or race to A. gubernator." In nearly all of the adult male redwings collected at Regina and Madison (above) one or more of the innermost (or proximal) middle (or greater) secondary wing coverts (which comprise the buffy row of feathers bordering the



Figure 1. Some typical representative patterns of individual pigmented proximal middle wing coverts selected from a number of birds to show the variation (all left wing, dorsal view).

red epaulet) exhibited variable patterns of black and buff (see Figure 1). Being intrigued by the regularity of the patterns of pigmentation, I made the following observations of this minor aspect of the plumage of A. phoeniceus.

The extent of melanic pigmentation on the proximal coverts of the birds in my samples varied from a small spot on the medium web of the innermost or first feather to complete pigmentation of the first, second, and rarely third feather in this row. Whatever the pattern in an individual bird, it tended to be the same, though reversed, on comparable feathers of the other wing. A high degree of such symmetry was exhibited by 64 per cent of the 100 birds collected at Regina (above). The others had patterns that were considered to be asymmetrical. Moreover, in about 70 per cent of the sample a regular progression of pigmentation from medial to lateral was evident: pigmentation was complete on the median web of the first feather before it appeared on the lateral web at all, and pigmentation was complete on the entire first feather before it appeared on the median web of the sample of the next feather. Idealized progressive pigmentation patterns for this group (67) are indicated in Figure 2.



Figure 2. Stylized pigmentation patterns of first and second median coverts, and distribution in one sample of 67 that were the same on both wings (left wing, dorsal view).

	Sample
Inner web incomplete	6
Inner web complete, no black outer web	3
Inner web complete, outer web incomplete	20
Whole feather complete, no black second feather	11
First feather complete, incomplete inner web second feather	24
First feather complete, complete inner web second feather	3
First feather complete, incomplete outer web second feather	0
	Inner web incomplete Inner web complete, no black outer web Inner web complete, outer web incomplete Whole feather complete, no black second feather First feather complete, incomplete inner web second feather First feather complete, incomplete inner web second feather First feather complete, incomplete outer web second feather

These patterns generally conform to Landauer's rule (1930: 80) for asymmetry of individual feather patterns in domestic fowl in which the larger pigment area of asymmetrically marked feathers is toward the main axis of the body and in which the left body side is the mirror image of the right one.

A system of deposition of melanin within a feather is suggested by these various patterns, and this may be indicated by Figure 3, in which progressive stages are shown by the letters a to e, and the direction of pigmentation by arrows. It is suggested that this apparent progressive pattern of pigmentation has some relation to pigmental invasion of a



Figure 3. Apparent progressive development of pigmentation within proximal wing coverts.

feather, although depigmentation of black feathers (which happens in a sense when immature males acquire their first adult plumage) could be equally the case. Since black color appears to be a primitive character in the Icteridae (Beecher, 1950), the latter may well be the case, in which instance the arrows and letters in Figure 3 can simply be traced in reverse to indicate the gradual loss or present tendency toward reduction of black color.

Comparison of 97 adult male redwings collected at Regina (above) with 97 collected at Madison, Wisconsin, showed a distinct difference in extent of pigmentation of these feathers. The innermost feather was all black in 36 per cent of the Madison and in 56 per cent of the Regina birds. Furthermore, in the Regina birds, 44 out of 55 that had the first feather all black showed some black in the next feather, whereas in the Madison birds only three out of 35 in which the first feather was all black had some black on the second feather. These data suggest that the extent of black color on the middle wing coverts of the redwing

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may have significance at the subspecific level generally, and also the possibility of a cline, particularly in view of the appearance of a western race in which this character appears to have reached its maximum extent (A. p. californicus). In this race black middle coverts, or at least broad black tips on the coverts, are a diagnostic trait (Ridgway, 1902: 326-330), and in a supposed Mexican race, A. gubernator grandis (Nelson), the middle coverts sometimes show "black only on tips of innermost coverts" (Ridgway, *ibid.*). The specimens from Regina have been considered to be A. p. arctolegus according to Snyder and Lapworth (1953), while those from Madison are A. p. phoeniceus, with tendencies toward arctolegus (Beer and Tibbitts, 1950). It would be desirable to check this trait in other races.

A number of tests were made in an attempt to determine whether the pattern of pigmentation remained similar from year to year in an individual. On 5 September 1952 I plucked and preserved the first (proximal) middle coverts of three captive adult males. One male had feathers that were all black—on 12 October these had regrown as all black feathers and were again plucked and saved. On 23 November the



Figure 4. Actual patterns of successive feathers produced by forced molt in captive birds (innermost covert).

regrown feathers were again all black. The second bird had feathers that were incompletely pigmented and asymmetrical, with a light central area on the lateral web (see Figure 4, A). On 12 October these had regrown as all black feathers. The third bird had feathers that were all black on the median webs and on the outer edge of the lateral webs (Figure 4, B). On 31 October one feather had regrown to a similar pattern; the other was nearly all black. It is interesting to note that the tendency in these experiments was for an increased amount of black color following successive forced molts.

Experiments on the Degree of Red Pigmentation of the Wing Coverts

It is well known that the amount of red color in the wing coverts or "epaulets" of the redwing varies between adult individuals, and is especially variable and much reduced in juveniles and immatures (Dwight, 1900; Allen, 1914; Wright and Wright, 1944). The immature male attains the full red epaulets of the adult (as well as the rest of the plumage) late in its second summer. This change occurs with the postnuptial molt in late July and August (Dwight, *op. cit.*), at a time when gonadal activity is at a minimum (Wright and Wright, *op. cit.*). This suggests that sex hormones are not the responsible agents for regulation of red pigmentation. Some brief experiments which I made in 1949 and 1952–1953 (at the University of Wisconsin Zoology Department) may be of interest in this connection.

The effects of forced feather replacement by plucking, castration, and the administration of testosterone propionate were tested on captive males with the following results. The normal dull orange-brown epaulets of an immature male were plucked following castration on 3 May 1949; the feathers soon regrew as a paler deep brownish-orange, showing a lower level of red pigment. Subcutaneous administration of a pellet of male hormone showed no effect on the next regrowth of feathers plucked from the opposite wing on 7 June; these grew in with much the same color as the previous forced feathers.

Similar results were observed in an adult male. Following the plucking of normal scarlet epaulets and castration on 3 May, epaulets regrew that were orange in color. Male hormone was administered, the other epaulets were plucked on 7 June, and again the renewed feathers were a shade of orange and much paler than normal. Quite similar results were obtained with a normal adult control bird: scarlet epaulets plucked on 22 May regrew as orange to orange-brown; epaulets plucked again on 7 June regrew generally as orange. However, epaulets plucked from a castrate adult male on 6 April regrew (by July) with more red pigment apparent, although below normal level, than in any of the others. Although there is no way of evaluating the dietary effect upon these caged birds, the above evidence would seem to suggest further that the male hormone, at any rate, is not the active agent regulating production of red pigment in this species.

During the period from March 1952 to April 1953, a number of additional trials were made on birds in captivity in order to determine whether the time of year might show some influence on the production of red pigment in the epaulets. Males were kept in captivity for up to eight months and were maintained as usual on a standard poultry "scratch-feed" diet. Epaulets were plucked to force regrowth of feathers throughout this period, and in general results were as above; the feathers that regrew tended to be much less red than normal, and subsequent pluckings on the same bird yielded progressively paler plumage, so that a male that had normal scarlet epaulets when captured in July would by March bear feathers that were almost yellow in color (and frequently spotted with black). However, in one case feathers that regrew following plucking on 5 September were more red than those that regrew following plucking on the previous 18 April. In three birds that were allowed to go through a normal molt (in late July-August), the new epaulets were much less red than originally but were definitely above the level obtained by forced molts before and after this period. This may mean merely that the normal molting process permits greater production of red in the feathers, or it may mean that there is a physiological mechanism geared to the normal molting season. The highly variable epaulet plumage that is assumed by immature males in their first winter molt in late summer (varying from yellow to reddishorange) may be related to such a cause. Inasmuch as carotenoid pigments (which produce the yellow and red color in the feathers) are available to birds mainly through plants (Fox, 1953), selection of food during the time of the molt may also influence the production of red in these feathers.

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LITERATURE CITED

ALLEN, A. A. 1914. The Redwinged Blackbird: a study in the ecology of a cat-tail marsh. Proc. Linnaean Soc. New York, 24-25: 43-128.

BAIRD, S. F., T. M. BREWER, and R. RIDGWAY. 1905. A history of North American birds. II. Little, Brown and Co., Boston.

- BEER, J. R., and D. TIBBITTS. 1950. Nesting behavior of the Red-winged Blackbird. Flicker, 22: 61-77.
- BEECHER, W. J. 1950. Convergent evolution in the American orioles. Wilson Bull., 62: 51-86.

DWIGHT, J., JR. 1900. The sequence of plumage and moults of the passerine birds of New York. Annals New York Acad. Sci., 13: 73-360.

- Fox, D. L. 1953. Animal biochromes and structural colours. Cambridge Univ. Press, England.
- LANDAUER, W. 1930. Studies on the plumage of the Silver Spangled Fowl. III. The symmetry conditions of the spangled pattern. Bull. Storrs Agr. Expt. Sta., 163: 71-82.
- NERO, R. W. 1954. Plumage aberrations of the Redwing (Agelaius phoeniceus). Auk, 71: 137-155.
- RIDGWAY, R. 1902. The birds of North and Middle America. Part II. Bull. U.S. Natl. Mus., #50.
- SNYDER, L. L., and E. D. LAPWORTH. 1953. A comparative study of adults of two Canadian races of Redwings. Canad. Field-Nat., 67: 143-147.
- WRICHT, P. L., and M. H. WRICHT. 1944. The reproductive cycle of the male Red-winged Blackbird. Condor, 46: 46-59.

Saskatchewan Museum of Natural History, Regina, Saskatchewan.