EFFECTS OF NATURAL ABRASION AND OXIDATION ON THE COLORATION OF FLICKERS

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In the course of a recent study of flickers (*Colaptes*) I have found it desirable to investigate, somewhat more fully than is usually done, changes that occur in the color of the plumage between molts. This matter of "wear" has been mentioned or discussed by many authors, for students of avian systematics find that consideration of it is necessary in most of their studies of variation in color.

It is now well established that a feather once mature is dead and cannot be affected thereafter by the bird's physiology. As only those features of coloration that relate to the physiology of the bird are of use in systematics and certain other studies of variation, workers should be alert to recognize and rule out of consideration changes that are direct results of external factors. But this is often a difficult thing to do accurately. The usual method employed by systematists is comparison of birds showing approximately equal degrees of "wear" in the plumage. In a large proportion of cases, individuals taken at about the same time of year are satisfactory for comparison, though differences in such factors as breeding season and habitat sometimes necessitate special caution.

Thus, in a general way, considerable attention has been paid to seasonal differences in coloration resulting from external influences. It has been shown that the loss of parts of feathers sometimes decidedly alters the coloration and color pattern of a bird's plumage. In addition to the observed loss of structure, changes in color have been thought to result from "fading" of the pigment that remains.

It was my object to determine by experiment, as well as by examination of museum skins, the relative importance of abrasion and sunlight in effecting changes in the coloration of the plumage of flickers. Furthermore, I wished to test their differential effects on the several colors and pigments present in the feathers. From information on this matter, one should be able to predict the way in which coloration of many other kinds of birds would be altered by any similar set of conditions.

In other studies, as yet unpublished, I have shown that the colors of flickers are produced by two classes of pigments, melanins and carotenoids. These two types differ considerably in their chemical composition, physical condition, distribution in feather parts, physiologic relations in the bird, and manner of deposition. The melanin pigments produce the black and brown colors and may be present in any or all of the three principal kinds of structures of a feather, the shaft, rami, and barbules. The bright reds and yellows of flickers result from carotenoid pigments. They may occur in the shaft and rami but apparently are absent from the barbules. Sometimes both carotenoids and melanins are found in the same part of a feather.

For the experiments on abrasion and fading, feathers were plucked from museum skins collected within the previous twenty-seven months and kept in darkness almost continually since that time. Two feathers of each kind were taken, from adjacent follicles when possible, and these were carefully compared for detection of possible slight differences in coloration. One feather of each sample was put in an envelope, which was laid away in a light-proof specimen case kept at room temperature. The other feather of each kind was fastened with one or two small strips of transparent adhesive tape to a gray, cellophane-covered cardboard, which was then taped on the outside of a south-facing windowpane at Berkeley, California; in this situation the feathers received sunlight most of the day. The flight feathers were fastened with their under surfaces out-

ward, and all feathers were entirely exposed to the action of air, sunlight, rain, and wind, except for a small part of the vane of each rectrix, which was covered by the head of a thumb-tack. Abrasion was impossible because each feather was securely taped to the cellophane that covered the cardboard; abrasion from rain is considered to be negligible. The feathers were exposed in this manner from September 30, 1938, until November 3, and from December 8 until February 8, 1939. A record of the feathers tested, and the results of examination of them on February 8 are given below. Unless otherwise indicated, the feathers were typical of the species. Names of colors with initial capitals are taken from Ridgway (Color Standards and Color Nomenclature, 1912), and the descriptions apply only to the pennaceous surfaces exposed in this study, unless specifically stated otherwise.

Colaptes cafer (original no. 411, F.H.T.), adult male, October 17, 1936, Walnut Creek, Contra Costa County, California:

Rectrix.—Control feather, between Scarlet and Grenadine Red, except for black distal end. Experimental, Strawberry Pink, much paler than control, except part of vane covered by thumb-tack, which is same color as control; black tip almost imperceptibly browner.
Primary.—Control, between Grenadine Red and Bittersweet Orange. Experimental, considerably paler than Shrimp Pink.
Interscapular.—Control, black bars alternating with broader interspaces of a hue between Wood Brown and Drab; shaft and rami pink. Experimental, brown regions slightly paler than control, barbules appearing slightly more brownish, less blackish; black regions apparently unchanged; carotenoid color of shaft and rami much paler.
Breast.—Control, dusky Pale Salmon Color with black subterminal spot. Experimental, melanic pigmentation of pennulae (slender distal parts of barbules) and of black region unchanged; carotenoid color much paler.
Throat.—Control, Pale Neutral Gray (mass effect on throat of bird) resulting from colorless rami and bases of barbules in combination with black pennulae. Experimental, pigmentation of pennulae slightly browner.
Crown.—Control, between Brussels Brown and Drab. Experimental, black melanin of pennulae and brown melanin of rami unchanged in color; shaft and rami paler and browner, apparently because of much paler carotenoid color.
Malar.—Control, rami in distal part of feather swollen, without barbules, and Spectrum Red in color; middle region of feather buffy. Experimental, red rami unchanged in color; pennulae or buffy region paler brown; black melanin in downy pennulae unchanged.

Colaptes auratus (feathers from several specimens):

Rectrix.—Control, Light Cadmium, with black tip. Experimental, lost; examination shortly before experiment ended showed it much paler than control.
Interscapular.—Control, similar to that of *cafer,* but carotenoid color yellow instead of pink. Experimental, changed as in *cafer.*
Breast.—Control, mostly a hue near Light Pinkish Cinnamon, but browner and more dusky; subterminal black spot; tip nearly white; rami and shaft yellow. Experimental, brown pigment slightly paler than in control; black region unchanged; carotenoid color almost lacking.
Throat.—Control, Light Pinkish Cinnamon. Experimental, unchanged.
Malar.—Control, black. Experimental, mostly unchanged, but extreme proximal part of pennaceous region considerably browner than in control.
Nuchal crescent.—Control, rami of terminal part swollen, without barbules, and Spectrum Red; proximal pennaceous part gray. Experimental, red rami unchanged; black melanin of gray region slightly browner.

A pink secondary taken from *Colaptes cafer* (original no. 679, F.H.T.), adult female, March 13, 1938, Davis, Yolo County, California: Control, between Orange-Pink and Grenadine Pink. Experimental, vane almost colorless; shaft paler than Orange-Pink.

An orange rectrix from atypical *Colaptes cafer* (no. 69417, Mus. Vert. Zool.), adult male, June 29, 1936, Rapid City, Pennington County, South Dakota: Control, Salmon-Orange. Experimental, between Bitterweet Pink and Safrano Pink.

Summarizing the results of this experiment, we find that the carotenoid colors of the flight feathers became much paler during their exposure. Examination of the feathers at intervals showed this change to be progressive. The yellow and the red flight feathers differed in that the yellow ones became paler but did not change otherwise. The red feathers became less yellowish as they paled, as did also the orange feather. It will thus be seen that Deakin's hypothesis (Amer. Nat., vol. 70, 1936, p. 587) that the orange hue found in certain flickers might result from fading of yellow pigment in heterozygous birds probably is not correct. In contrast to the reaction of the carotenoid pigments in the flight feathers, the red pigments of the malar feathers of *cafer* and the nuchal crescent feathers of *auratus* showed no observable change in color or tone, either when viewed with the naked eye or when examined with the 16 mm. objective of a compound microscope.

Of the melanic colors, the blacks (as in the malar feathers of *auratus,* the subterminal spots of the feathers of the breast, and the bars of the interscapulars) showed either no change or one that was scarcely perceptible. Most of the grays and browns became slightly paler, and the former turned more brownish.

These changes in both kinds of pigments probably resulted from oxidation, for abrasion was negligible in the experiment. The role of light in the oxidation of the melanins seems to be small. In contrast, there is evidence that light is important as a catalyst in the oxidation of the carotenoids in the feathers. This evidence is the difference in color between parts of the experimental feathers. The morphologically lower sides of the flight feathers exposed to the action of both light and oxygen became pale, as described above. In contrast, the parts of the vanes covered by the heads of thumbtacks, and the upper sides of the shafts, which were facing the cardboard, remained practically unchanged. As these parts were exposed to oxygen but scarcely, if at all, to light, it seems reasonable to conclude that light was the critical factor in the paling of the other parts of the feathers. The keratin in which the carotenoid pigments lie probably protects them from much contact with oxygen. Some air may be present in small intercellular spaces in the feather, and minute amounts perhaps reach the pigments through the keratin or through pores in it, but not enough is known of the morphology of these feathers to decide which suggestion is more probable. It is known, however, that carotenoids are very susceptible to autoxidation in air, even at room temperatures, and that light greatly facilitates this process (Bogert, *in* Gilman's "Organic Chemistry," vol. 2, 1938, p. 1183). That the carotenoid pigments in the feather are partly protected in some way, as by the keratin filtering out certain light rays or preventing contact with oxygen, seems highly probable; irradiation with ultra-violet, according to Bogert, has been found to destroy unprotected carotene (a carotenoid pigment) in three hours. The purity of the pigments in the feather and their physical state may also be important factors in their resistance to change of color.

At present I am unable to explain the lack of change in the red color of the malar and nuchal crescent feathers. The structure of the carotenoid-containing parts of these feathers may be such as completely to prevent contact of the pigments with oxygen. The decrease in yellowness of the flight feathers of *cafer,* when they are exposed to light, may be explained in one of two ways on the basis of the fact that both red and yellow pigments are present in the newly grown feather (unpublished data). Either (1) the yellow pigments oxidize more rapidly, or (2) the yellows, being present in smaller amounts, become completely oxidized (rendered colorless) before the reds do. Perhaps both factors contribute to the result, but because the experimental orange rectrix, which contained much less red than yellow pigment, also became slightly redder, differential rate of oxidation is the more probable explanation.

It should be profitable to compare the results obtained in the experimental exposure of feathers with the colors found in the plumage of a wild-taken, breeding bird, for this should provide some idea of the importance of abrasion in producing changes of color in free-living birds. In making such a comparison I have used a male *C. cafer collaris* (no. 69437, Mus. Vert. Zool.) taken July 16, 1936, at an altitude of 5300 feet on Twelve-mile Creek, Washoe County, Nevada. This bird probably had recently finished caring for its young, and its plumage shows a large amount of change due to exposure. The locality where it was taken is one with intense sunlight.

The black regions of the feathers of this specimen seem nearly unchanged in color. Microscopic examination shows scarcely any effect of abrasion, which would be evidenced by loss of barbules or by wearing of the rami and shaft; the color of the feather parts appears just as dark as in the experimental feathers and in feathers from fresh-plumaged birds.

In contrast to this condition, the brown and gray regions of the feathers appear considerably paler to the naked eye than do those of both the experimental and the control feathers; the tips are most strongly affected. An indication of the change in color that has occurred is afforded by comparing the distal brown region of five recently grown interscapulars with the same parts of nearby feathers that had been regenerated by the bird in the molt of the previous autumn. The newer feathers are Tawny-Olive, the old ones slightly browner than Vinaceous-Buff. On microscopic examination, these changes are seen to result principally from two things: (1) a loss of barbules, leaving considerable sections of rami bare and exposing the almost colorless bases of barbules and the sides of the rami; and (2) wearing away of the melanized upper surfaces of the rami, exposing the unpigmented parts beneath. The pigment in the barbules appears only a little paler in color than does that in barbules of unworn feathers. This indicates that oxidation of pigment plays relatively little part in the changes of melanic colors in the flickers, although it probably is facilitated by the exposure of melanin to the air in the wearing away of keratin.

In addition to the causes of paling just described, a paler "mass effect" in certain groups of feathers (those of the throat, for example) is achieved in part by exposure of the paler basal parts of feathers through loss of pigmented structures in the overlying ones. In other groups of feathers, particularly those of the wings and back, a differential loss of black and brown parts of the feathers results in a darker general effect. As other observers have noticed in certain other species, the black bars on the flight feathers are abraded much less rapidly than are the brown regions between them. It seems possible to me that the dense deposits of melanic pigment in the black rami and barbules serve to strengthen these parts to an extent such that they are less easily broken than are the much less heavily pigmented brown rami and barbules.

The red pigments of the malar regions and nuchal crescent of the Nevada bird, appear unchanged, although each malar region as a whole appears lighter in color because loss of the tips of the rami has partly exposed the pale buffy middle regions of the feathers. The effect on these feathers of several months exposure to sunlight is, thus, negative, as was true with the experimental feathers.

The red color of the outer rectrices, those most exposed to light, is considerably duller, paler, and less orange than that of the inner ones. Specifically, the colors are, respectively, between Scarlet and Peach Red but slightly redder than either, and a trifle redder than Grenadine Red. A corresponding difference exists between outer and inner primaries. The change in color of these rectrices and remiges is thus much less than that occurring in the experimental feathers, the difference between the two presumably

resulting from a difference in length of time of exposure to intense light. The differential between outer and inner feathers is further evidence of the importance of sunlight in the oxidation of the carotenoids.

The proximal part of the upper surface of the shaft of each proximal secondary exhibits a pattern of alternate sections of pale pink and more intense pink. I have seen this same coloration in other breeding flickers, particularly those from regions of strong and long-continued sunlight. The explanation seems to be that the black bars of each of several secondaries protect the pigment in the shaft of the feather beneath to a greater degree than do the less heavily pigmented, brown interspaces, for the pale pink sections always coincide with the brown regions, and the more intensely pink sections with the black regions, of the overlying feather. The basal parts of the shafts of the proximal secondaries are little altered in color, for they are protected by several coverts and scapulars. In this Nevada-taken specimen, the distal parts of the shafts of secondaries nine and ten, which parts probably are exposed to light most of the time, are nearly colorless.

The pinkish hue found in newly grown feathers of breast and back is almost absent from the feathers of the breeding Nevada specimen, their condition in this respect being like that produced in the experimental feathers.

SUMMARY

Experimental exposure to sunlight for sixty-five days of several kinds of feathers from flickers in fresh plumage resulted in a paling in their coloration. The carotenoid colors (reds and yellows) of all feathers except the red malars and nuchal crescent feathers were strongly affected; the latter type of red apparently was unaltered. The changes in color probably result from slow oxidation under the influence of sunlight. The melanic hues (browns, blacks, and grays) were only slightly affected by the exposure.

Comparison of these results with the conditions found in breeding birds shows that the changes that take place in the carotenoid colors of free-living individuals are similar to those seen in the experimental feathers; the amount of change varies in inverse proportion to the amount of protection from sunlight. The changes in the melanic hues are principally a result of loss of pigment through abrasion; black regions scarcely change, because loss of pigment is slight and that which does occur is rendered imperceptible by the great concentration of black.

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