RELATION OF WING AND TAIL COLOR OF THE WOODPECKERS *COLAPTES AURATUS* AND *C. CAFER* TO THEIR FOOD

FREDERICK H. TEST

Department of Zoology
University of Michigan
Ann Arbor, Michigan 48104

The data presented in this paper were gathered several years ago to aid in solving certain problems arising in a study of variation and evolution of the coloration in natural populations of flickers. Other work has intervened and it now seems likely that I shall not continue these studies. They are published now for their relation to the recently revived interest in interbreeding between well differentiated populations of animals. The variability in coloration of these woodpeckers has attracted attention from students of evolution, geographic distribution, and genetics for many years (Allen 1892; Bateson 1913; Mayr 1963). Despite this interest, almost nothing has been known of the physiology of the red and yellow pigmentation, in which some of the chief variations occur. Such knowledge appears to be basic to a proper understanding of other aspects of the problem. Examination of some 2000 specimens, mostly study skins, and experiments with captive birds have provided most of the information here reported.

Two well differentiated populations occupy the forested areas of North America, *Colaptes auratus* (Linnaeus) in the Great Plains and eastward, and *C. cafer* (Gmelin) west of the Great Plains. One of the striking differences between them in coloration lies in the color of the undersides of the large flight feathers of wings and tail. In the former these are bright yellow, in the latter bright red.

It has been shown (Test 1942) that the red and yellow colors in the flight feathers of *Colaptes auratus* and *cafer* are produced by mixtures of carotenoid pigments. Carotenoids are synthesized by plants, but there is no positive evidence that animals are able to produce them from simple colorless substances (Goodwin 1952; D. L. Fox 1953; H. M. Fox and Vevers 1960). A number of species, including several birds, have been shown experimentally to be dependent on ingested food for their carotenoid pigments. Brockmann and Völker (1934) found, in studying the feather pigments of canaries, that some modification of carotenoids may take place before the pigments are deposited, and Kritzler (1943) provided additional evidence of the same sort. Other studies producing similar data have been summarized by D. L. Fox and by Goodwin (op. cit.).

DEPENDENCE OF CAROTENOID PIGMENTATION ON INGESTED PIGMENTS

Although no bird has yet been shown to perform the basic syntheses in the formation of their carotenoid pigments, it seemed desirable to test this point in *Colaptes*, especially as no experiments on woodpeckers have been reported.

The birds used in the feeding experiments were housed in indoor cages large enough for short flights. Before being caged, they were trained to the presence of humans and to eating the special food provided by a method similar to that employed by aviculturists with insect-eating birds, as suggested to me by E. C. Kinsey, of Manor, California. One or two weeks usually passed before they learned to take the food by themselves. As the bird usually was more or less emaciated by this time, it was not released in the large cage until part of the lost weight had been regained. A separate food cup for each individual was found desirable, and no more than two birds were caged together.

The basic diet was a modification of one used successfully by G. B. Happ of Principia College. It consisted of: 450 g pheasant meal, 150 g crissel (fine), 50 g "ant eggs," 50 g "dried flies," 112 g suet (rendered), 19 ml cod-liver oil, and 4 g calcium lactate. These ingredients were mixed dry and kept at about 54°F. About once a week a portion was mixed with half its volume of boiled, peeled potato, then dried to keep it from becoming moldy in the bottoms of the food-cups. The birds, once they had learned to eat it, readily took this mixture, placing the tip of the bill close to, or in, the food and ingesting the small particles with rapid movements of the tongue.

This food contained only small (unmeasured) amounts of carotenoids. The first four items listed above were obtained from Spratt's Patent Limited which provided the information

TABLE 1. Progressive paling in carotenoid color of successive feathers regenerated by adult female *C. cafer* in captivity on carotenoid-poor artificial diet. Color terms from Ridgway (1912).

Feathers	Originals: Removal	Originals: Color	Regenerants: Date examined	Regenerants: Color
retrix left 4	plucked Mar. 17	between Scarlet and Grenadine Red	May 2	between Deep Chrome and Capucine Yellow
secondary left 5	plucked May 16	Bittersweet Orange	June 18	between Mustard Yellow and Primuline Yellow
retrix left 4	plucked May 16	between Deep Chrome and Capucine Yellow	June 18	between Mustard Yellow and Primuline Yellow
secondary right 4	plucked June 18	Bittersweet Orange	July 9	Barium Yellow
primary 1 in both wings	molted June 18	Bittersweet Orange	July 9	Barium Yellow
primary 2 in both wings	molted June 25	Bittersweet Orange	July 17	between Barium Yellow and Naphthalene Yellow
primary left 3	molted July 3	Bittersweet Orange	July 17	Naphthalene Yellow

that pheasant meal was largely wheat flour (not whole wheat), with some dried, ground beef and ground bone. The crissel was powdered dried beef, with a little ground bone. "Ant eggs," as they are known commercially, were dried ant pupae, in most of which metamorphosis had not proceeded far. The "dried flies" usually were large ostracod crustaceans, but once they were aquatic Hemiptera.

This diet contains little carotenoid pigment. Traces of carotene and xanthophyll may occur in the meat. Although analyses of two species of wheat (Markley 1937) showed the total carotenoid content to be 2.4–3.7 ppm, the refined flour in my pheasant meal probably was nearly free of carotenoids. Euler et al. (1934: 86) reported carotene in "Ameiseneier," but they do not state whether their material consisted of true eggs or of dried pupae; the latter seems more probable. Ostracods and aquatic hemipterans probably also contain traces of carotenoids. White potato tubers may lack these pigments altogether. Cod liver oil almost certainly contains carotenoid pigment of some kind. I have not found identification of the yellow color in the liver oil of cod, but Lederer (1935:21–22) mentions that xanthophyll, carotene, and astacin have been found in the livers of certain other fishes.

Flickers, both *auratus* and *cafer*, fed on this diet for two to four months or longer, regenerated feathers in which carotenoid color was reduced to very pale yellow. Records (table 1) for a female *cafer* captured 15 March 1939 show a series of progressively paler and less reddish feathers grown over the next four months and indicate clearly a gradual decrease in carotenoids available for feather pigmentation. Less extensive results from other individuals were similar. This is in contrast to Kritzler's results (1943) with bishop birds, which continued to deposit carotenoids, probably because of larger fat deposits which served as storage sites for pigment later transferred to the feathers.

PIGMENT DEPOSITION WHILE ON A CAROTENOID-RICH DIET

The next experiments were designed to determine whether feathers regenerated while on a diet rich in carotenoid pigment would be more heavily pigmented. For these experiments the same dry mixture was used, but the boiled potato was replaced with raw carrot root. The whole root was shredded fine and thoroughly mixed with the rest of the food.

Carrot roots are known to be rich in carotenoid pigment, which is responsible for their orange color. The pigment is principally carotene, but a small amount of xanthophyll also is present (Barnes 1936). No determination was made of the amount of pigment in the carrots used, but differences in color between lots indicated considerable variation. An approximate figure can be found, however. Barnes (op. cit.) learned that the carotene content of market carrots varied from 1.15 mg to 3.76 mg per 10 g fresh weight of roots. The carrots used in my experiments were picked for their high color, so it seems conservative to assume for them an average carotene value of 2.5 mg per 10 g of roots. Assuming that each bird ate an equal amount (very little food was lost), it received an average of about 6.75 mg of carotene each day. Of xanthophyll, Brockmann and Völker (1934:197) state that

100 g of fresh carrots contain 0.39 mg of lutein. On this basis, each flicker received about 0.11 mg of lutein per day in addition to the carotene.

The carrot-feeding experiment was first tried with the female *cafer* cited previously, when she was undergoing the annual (autumn) molt. At that time the feathers she was growing were almost colorless (as regards carotenoid color), for her diet had been low in carotenoids. On 26 September the potato in her food was replaced with carrot for 44 days, and in this period the bird regenerated three primaries. These new feathers were orange, close to Capucine Yellow (all capitalized color names are from Ridgway 1912), much more intensely colored than the extremely pale (between Pale Pinkish Buff and Pinkish Buff) primaries and secondaries which were grown while the bird was eating the carotenoid-deficient food.

On 10 November carrot feeding was stopped until 5 December when carrot was again put in the food. Examination on 29 November showed two growing primaries; right 10 was 25 mm long (measured from the surface of the skin), and left 9 was 47 mm. The distal part of each feather thus was regenerated while the bird was eating the carotenoid-deficient diet, their proximal parts after carrot was put in the food. When growth was completed, the distal 33 mm of right 10 and 55 mm of left 9 were decidedly paler (near Pale Yellow-Orange) than the proximal parts. The position of the short zone of transition between the two colors in each feather agreed closely with the calculated length of the feathers on 5 December, as judged from the average growth rate (Test 1945), and indicated that when an abundance of usable carotenoid pigment is added to the diet, pigment is deposited in growing feathers almost immediately. The narrowness of these transition zones showed that maximum concentration of the pigments was reflected in growing feathers within a few hours.

Later experiments with this same bird and with two other individuals of *cafer* produced similar results, both when they were molting and when they replaced plucked feathers.

Similar experiments were tried with two individuals of *C. auratus luteus*, in which the wing and tail feathers were bright yellow, varying from Primuline Yellow in the rectrices to Amber Yellow in the proximal secondaries. Both birds were captured in Indiana and shipped to Berkeley for study, where they were first fed the carotenoid-deficient diet. A juvenile female which reached Berkeley the middle of July grew middle secondary feathers in the course of normal molt, while on this diet, which were extremely pale (Marguerite Yellow). From the other bird, an adult female, a primary was plucked in January. The bird died an accidental death late in the month but the new feather had grown enough to show that little carotenoid pigment was being deposited.

In the course of her molt the above juvenile was changed to the carotenoid-rich diet. Feathers partly grown at the time of this change were bicolor when mature, with the distal end extremely pale (Marguerite Yellow) and the proximal part bright (between Empire Yellow and Apricot Yellow). The zone of transition between the two hues was about 3 mm in breadth. Feathers in which all growth was made while the bird was on the carrot diet and soon thereafter were bright yellow throughout.

SOURCES OF CAROTENOIDS FOR WILD *COLAPTES*

With flickers shown to be dependent on ingested food for the carotenoid pigmentation of their feathers, it is pertinent to inquire into the natural sources of these pigments. This matter is especially important in attempting to learn the causes of certain atypical colorations which are sometimes encountered in wild individuals.

The uniformity of carotenoid coloration in *auratus* from individual to individual over most of its extensive range through the greater part of the forested regions of Canada and the eastern half of the United States suggests that its source of pigment is widespread and present in at least moderate abundance at the time of molt. In the extract of pigment from flight feathers of this species, both xanthophylls and carotene occur (Test 1942). They are specific pigments identical with, or closely similar to, known carotenoids which are of more or less widespread occurrence in plants. Hence, these pigments probably are present in many items this species uses as food.

The principal food items of *auratus* were reported by Beal (1911) on the basis of examination of 684 stomachs representing all months of the year and many sections of the country. Ants were found to comprise 50 per cent of the food. Other common items were fruits and insects, listed here in approximate order of decreasing importance: *Rhus* spp., bayberry (*Myrica*), Coleoptera, sour gum (*Nyssa*), wild cherry (*Prunus*), hackberry (*Celtis*), Orthoptera, wild grape (*Vitis*), dogwood (*Cornus*), lepidopterous larvae, *Rubus*

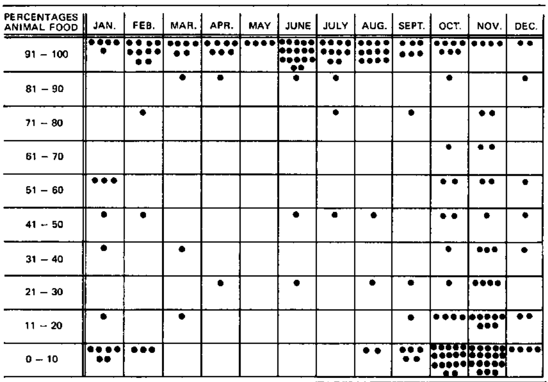

FIGURE 1. Proportions, by volume, of animal material in food eaten by 210 wild individuals of *Colaptes cafer* in different months. Each dot represents one stomach examined.

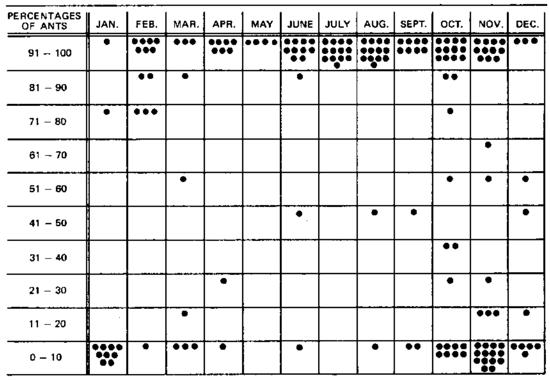

FIGURE 2. Proportions, by volume, of ants in the animal food of 163 wild individuals of *Colaptes cafer*. Each dot represents one stomach containing 5 per cent or more of animal food.

spp., acorns (*Quercus*), corn (*Zea mays*), elderberry (*Sambucus*). In addition there were fewer records of a wide variety of fruits and seeds of wild and cultivated plants and some other arthropods. The food of *cafer* was found to be essentially the same.

The carotenoid content of these food items is not known precisely, but it probably is fairly high. I have been unable to find a record of the carotenoids in adult ants. A few members of the other groups of insects mentioned have been studied by various investigators (Lederer 1935; Kilby 1965), and nearly all were found to contain carotene, many of them xanthophyll, and a few lycopene. Palmer's summary (1922) of analyses of many fruits and seeds suggests that most of those eaten by flickers contain both carotene and xanthophyll.

The natural food of flickers certainly is sufficiently rich in the requisite types of carotenoids to supply the pigment which is deposited in regenerating feathers. Probablv little pigment is necessary to color the small amount of feather tissue available for pigmentation at any one time, for regeneration of new plumage is extended over about three months. Furthermore, flickers are not dependent entirely on pigment ingested in this period but can draw upon stores in the body fat and liver.

DISCUSSION

The question arises as to why *Colaptes cafer* and *C. auratus* produce, respectively, red flight feathers and yellow flight feathers. Several possibilities come to mind. Dependent as they are on food for their carotenoid pigment, do the two species ingest different pigments? From the wide variety of foods eaten by each kind, the probability that any individual also samples widely, and the uniformity of their red and yellow colors, it is likely that the answer is negative. Furthermore, when captives were fed on the same carotenoids, the two species grew differently colored feathers. It has been shown (Test 1942) that the red color in flight feathers of *C. cafer* results from the presence of red pigments not found in those of *C. auratus*; both species deposit yellow pigments. The main problem, then, is to learn the origin of these red carotenoids. Their properties, in so far as discovered, indicate that they are allied to certain red pigments occurring in other animals, including insects and birds. Most such red pigments are believed to be derived by oxidation from other carotenoids (D. L. Fox 1953).

A study of the stomach contents of *Colaptes cafer* based on records provided by the U. S. Fish and Wildlife Service showed (fig. 1) that most of its food in spring and summer was animals, and that in summer and early fall, the time of growing new feathers (Test 1945), ants constituted the main bulk of the animal portion (fig. 2). Although there is no information on the carotenoids in adult ants, it is possible that they supply a red pigment which the bird deposits in its feathers. However, as *C. auratus* probably has a similar seasonal shift in diet, and because the feeding experiments clearly demonstrated that the two species grew differently colored feathers on exactly the same synthetic diet, one must postulate that the two species treat the red pigment differently. Brockmann and Völker (1934) and Zechmeister and Tuzson (1935) have shown that some carotenoids which are deposited by certain vertebrates are decomposed or eliminated by others.

It is also possible that *cafer* has evolved the means of converting common yellow or orange carotenoids into red pigment, and that *auratus* lacks that ability. Such alteration of carotenoids is well known and provides the red pigments found in some aquatic crustaceans (Sørensen 1937) and the Ring-necked Pheasant, *Phasianus colchicus* (Brockmann and Völker 1934), for example.

The red feathers grown by my *C. cafer* captives, even when on the carrot-rich diet, were never as red as in wild-taken individuals. Together with the correlation between an ant-rich diet and the normal period of feather growth, this suggests that ants may supply some of the pigment needed for normal feather coloration in this species. The needed pigment may, perhaps, not be red, but might be a yellow or orange carotenoid in the form of a specific xanthophyll or carotene which serves as a precursor for the red pigment deposited by *cafer*. The ant pupae in the synthetic diet of my captives may have supplied enough pigment to redden the feathers; adult ants may be required to produce normal full coloration. If this hypothesis is correct, *auratus* obviously does not use the ant pigment(s) in the same way.

A similar situation has been shown by Kritzler (1943) to occur in certain bishop birds which, in the wild, deposited red pigment in their feathers. In captives fed on a seed diet one of these red pigments was no longer deposited. However, when tomatoes were added to their food, this normal red pigment was again incorporated in developing feathers of *Euplectes franciscanus* and *E. nigroventris*. *E. taha* and *Ploceus cucullatus*, on the contrary, showed no such change in pigmentation.

As red carotenoids are generally thought to result from the modification, largely through oxidations, of yellow and orange pigments, the inability of *C. auratus* to synthesize or utilize (whichever be true) red pigment in its flight feathers indicates a less complex, thus perhaps more primitive, condition of carotenoid metabolism than in *C. cafer*. It may be pointed out, however, that an occasional flicker found well within the geographic range of *auratus* and with all other characteristics normal for this population possesses a set of flight feathers in which several or all are reddish. Such specimens were taken 21 February 1912 at Jackson, Alabama (U. S. Fish and Wildlife Service 231072); Shellmound, Tennessee (Chicago Acad. Sci. 6395), 19 November 1937; Highland Park, Illinois, lacking data on month and day in 1940 (Chicago Acad. Sci. 9192); Ithaca, New York (Cornell Univ. 10133), taken in the breeding season on 2 June 1941; Danbury, Connecticut, 6 October 1905 (Amer. Mus. Nat. Hist. 362063); Penikese Id., Massachusetts, 29 September 1889 (Mus. Comp. Zool. 245172). At its reddest the color is reddish orange, as in a specimen (Mus. Comp. Zool. 248862) taken 18 September 1909 at Brewer, Maine. It is different from that of normal *C. cafer* and from birds in the zone of hybridization between red-feathered and yellow-feathered flickers in being somewhat coppery. Through the courtesy of John T. Emlen I have also examined an adult (Zool. Mus. Univ. Wisc. 13784) similar to the last and taken at Madison, Wisconsin, on 4 August 1949. A molting juvenile killed at State College, Pennsylvania, on 25 July 1953 and kindly made available by Merrill Wood, also had several red feathers. Interpretation of the condition shown by these specimens is presently not clear, but it is unlikely to have resulted from genetic transfer from *C. cafer*.

SUMMARY AND CONCLUSIONS

Captive individuals of the yellow-feathered *Colaptes auratus* and red-feathered *C. cafer* fed on a standard balanced diet containing a low level of carotenoid pigment regenerated feathers which were progressively paler in carotenoid color. Loss to a minimal level of very pale yellow occurred over a period of two to four months as stores of pigment in fat, liver, and other organs were depleted and became unavailable for transfer to growing feathers. With addition of raw grated carrot roots to the food, both species again grew highly colored feathers, pigment levels in the developing feathers building to maximum in a matter of hours.

Using the carotene and xanthophyll in the carrots, *C. auratus* grew yellow feathers, while *C. cafer* produced orange-red ones, showing an impressive difference in their use of the same ingested carotenoids. Though they are dependent on ingested pigment for these colors, this evidence, together with the known similarity of natural food in the two species and the generally uniform color in each population over large geographic ranges, shows that the normal difference in the color of flight feathers in wild populations results from an important difference in carotenoid metabolism, not from the intake of different foods. However, evidence is presented which suggests that full expression of the red color of *C. cafer* may be dependent in nature on some pigment in ants, which form a large part of the food of flickers in the period of feather growth.

Evidence on the carotenoid metabolism of *C. cafer* shows that it is more complex, hence perhaps more highly evolved, than in *C. auratus*. The latter, however, apparently is able occasionally to produce and deposit red pigments in its flight feathers.

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