The Control of Color in Birds

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SYNOPSIS. The colors of birds result from deposition of pigments—mainly melanins and carotenoids—in integumentary structures, chiefly the feathers. The plumages of birds indicate their age, sex, and mode of living, and play important roles in camouflage, mating, and establishment of territories. Since feathers are dead structures, change of color of feathers is effected through divestment (molt) and replacement. The color and pattern of a feather are determined by the interplay of genetic and hormonal influences prevailing in its base during regeneration. Most birds replace their feathers at least once annually. Some wear the same kind of basic plumage all the time but others alternate a basic and breeding plumage, either in one (the male) or both sexes. Still others may have more than two molts, adding supplemental plumage at certain times in the plumage cycle. The varieties of patterns of molt, the kinds of plumage, and the colors and patterns of feathers among birds apparently are the result of several kinds of selection pressures working through evolution.

Birds are exceeded only by insects in geographical distribution. They have played important roles in the history and folklore of man, and all cultures have been enchanted by their astonishing variety of colors, especially that of the plumage.

Although most colored structures of birds are dead, they remain intriguing objects for study of the origins and maintenance of structural and color patterns. The pigment-producing cells of feathers are highly sensitive to changes in their environment, leaving a permanent record of their responses to various influences that act upon them in the course of development. Thus, feathers are excellent systems for analysis of biological patterns (Cohen, 1966).

Pigmented external structures of birds include feathers, beaks, combs, wattles, skin, eyes, and scales of legs and feet. Pigments also occur in the membranes surrounding various organs and tissues, and are secreted by the glandular wall of the oviduct to be incorporated into egg shells.

What is said here about feathers relates mainly to the adult-type, contour feathers; that is, those feathers forming the bulk of the definitive garb of birds. The plumages of young birds (natal down and juvenile plumage) are not of great significance for this presentation. I have attempted only to present a sampling of the information available about control of color in birds.

Throughout life, birds renew their plumage periodically. Some very large birds may molt some feathers at longer intervals, but most adult birds undergo a complete molt at least once annually. Additional molts, often partial, occur in many birds. It is by the loss and replacement that birds effect color changes of feathers if they change colors at all. Many simply replace old feathers with the same kind of feathers. Others undergo dramatic seasonal changes in plumage.

The vestures of birds indicate their age, sex, and mode of living. Survival may be enhanced in some whose plumage serves as camouflage. In many species the seasonal changes of plumage associated with molt are importantly related to reproduction. The nuptial (or alternate; see Humphrey and Parkes, 1959) plumage has a function in territorial aggression, or courtship display, or both.

FEATHER COLOR AND PATTERNS

It is obvious that feathers differ from one region to another on the surface of
adult birds. They are arranged in distinct units or tracts (e.g., breast, flank, wing primaries) and the feathers of a tract tend to be similar in morphology, but do show variation. The follicles producing the feathers of any one tract are arranged in highly ordered rows or pterylae.

The feathers of the different tracts tend to have different developmental histories (Holmes, 1935), and when a bird molts there is a characteristic order of feather loss within tracts (Humphrey and Parkes, 1959). Feathers also become competent to react to hormones at different times (Trinkhaus, 1953).

The feather is composed largely of keratin, an undefined proteinaceous material produced and exactly organized by epidermal cells shortly before they die. Variations in the structure of keratin to produce optical effects, added to variations in kind and distribution of pigments, are what produce feather patterns. Each individual feather pattern is subordinate to the general pattern of the entire plumage (Cohen, 1966).

Nature of Colors

No other vertebrates have the variety of colors and shades that birds have. However, their diversity of coloration is achieved by various combinations of a relatively small number of pigments and structural configurations.

Melanins. These are the most important of the pigments and are responsible for the dark, somber colors such as black, grey, brown, and related tints. Melanin also provides the dark background necessary for the perception of blue and green resulting from light scattering (Fox and Veevers, 1960).

Special cells of neural crest origin (Dorris, 1938), which have the potential to produce melanin, take up residence in the feather germs (as non-pigmented cells called melanoblasts), and as the barbs of a developing feather are formed these cells, now called melanocytes (Gordon, 1953), transfer their pigment to barb cells.

Differences in oxidation of the same substance, a propigment, lead to the development of different variations of melanin. The black and dark-brown pigments are known as eumelanin, or simply melanin, and the red, light-brown, and yellow melamins as phaeomelanin. Eumelanin is known to be formed by a two-stage oxidation of tyrosine under the influence of tyrosinase, a copper-containing enzyme (Fitzpatrick and Kukita, 1959). The exact cause of the difference in origin and composition of black and brown eumelansins is not known, but Dorris (1938) suggested that the intensity of color depends on the stage at which oxidation of tyrosine ends, since melanin was seen to appear first as small yellow granules, then become larger and simultaneously dark brown or black.

Melanins are usually in the form of granules about 1 μ or less in length. They have a definite structure, as revealed by electron microscopy (Schmidt and Ruska, 1961), but their form differs among feathers, as between feathers of cock and hen in domestic fowl (Carr, 1957; Trinkaus, 1948). Melanin granules from different breeds of fowl also differ in size, shape, and color (Willier and Rawles, 1940). A histological and chemical investigation of the feathers of 37 breeds of domestic fowl revealed that the melanin of black feathers was in the form of rod-shaped granules (0.5 to 0.6 μ by 1.0 to 1.3 μ), that of the background of blue feathers was in spherical granules (0.5 μ in diameter), and in buff and reddish feathers the granules were oval (0.7 μ by 1.0 μ) (Bohren, et al., 1943; Nickerson, 1946a).

The pinkish-brown color of the breast in the male chaffinch (Fringilla coelebs) has been attributed to the arrangement of phaeomelanin granules in groups with spaces between them from which light is reflected (Frank, 1939). Here is an example of what might be called a pigment-structural color.

Carotenoids. The bright colors—yellow, orange, and red—of eggs, eyes, portions of skin and adipose tissue, and feathers generally are due to fat-soluble, nitrogen-free
compounds, formerly known as “lipochromes”, but now called carotenoids. In contrast to melamins, carotenoids are not the products of special pigment cells. Their source, genesis, and manner of infiltration into the developing part of the feather are largely obscure. Carotenoids and their precursors are obtained by birds from their foods. The pigments are known to be dissolved in fat droplets in the early stages of development and as keratinization begins the droplets disappear, leaving carotenoids deposited in the barbs (Voitkevitch, 1966).

Some carotenoid pigments are united with protein. Such a union may make the pigment water-soluble, as is the case for the xanthophylls, lutein, and zeaxanthin, of the hen’s egg (Fox and Vevers, 1960).

Changes in the environment usually have a greater influence on the carotenoids than upon the melamins, but melamins are subject to fading, especially in birds of open areas; dark-brown feathers may fade to buff by the time they are molted (Parkes, K. C., personal communication). Diet is the most important variable with respect to carotenoids. Chickens on diets devoid of colored carotenoids produce nearly colorless yolks. The pink and red feather pigments of flamingos (Phoenicopteridae), the roseate spoonbill (Ajaia ajaja), and the scarlet ibis (Eudocimus ruber) result from ingestion of foods containing carotenoids (Fox, 1953).

Canaries maintained on carotenoid-free rations develop white feathers but will replace them with yellow feathers if switched to a diet containing xanthophylls or derivatives. Red feathers can be produced by canaries fed paprika, which contains capsanthin, and an even deeper red is produced when they are fed rhodoxanthin, a red carotenoid (Fox and Vevers, 1960).

The display plumages of many nuptial-colored male birds, such as those of the genus Euplectes, contain several carotenoids, whereas those in eclipse (basic) plumage are nearly devoid of such pigments. Some male birds will retain rich carotenoid stores in the liver and adipose tissues even after they have been maintained for nearly three months on carotenoid-free diets (Kritzler, 1943).

Other Pigments. A porphyrin, protoporphyrin, is present in the egg shells of many birds (Fischer and Linder, 1925). There is sometimes enough of a porphyrin (coproporphyrin III) to give a pinkish color to down feathers of owls and bustards (Völker, 1939).

A pigment, which is a copper compound of uroporphyrin III, called “turacin” (Church, 1893; With, 1957), found only in quill feathers of turacos, African birds of the family Musophagidae, is purpled normally, but is reputed to turn blue or leach out when exposed to rain. However, Chapin (1939) refutes this color change and never observed birds with faded feathers even in the wettest forests. The pigment will go into solution if the feather is dipped in an alkaline solution such as ammonia water. Many turacos do have a bright green pigment (turacoverdin), the only true green pigment known in birds.

A few feathers have pigments (probably porphyrins) which fluoresce in ultraviolet light. Feathers of the parakeets and some parrots (Psittacidae) show a yellow fluorescence (Völker, 1937).

Coloration is often the result of a mixture of pigments. The beak and skin frequently contain mixtures of carotenes and xanthophylls. An olive-green color in the beaks of mallards (Anas) is due to carotenoids in oil droplets together with melanocytes. Olive-green in feathers is often due to black melamins and yellow carotenoids juxtaposed (Fox and Vevers, 1960).

Structural Colors. Colors are called structural, as opposed to pigmentary, when the physical nature of a surface is responsible for the color. These are the iridescent and so-called “metallic” colors. Iridescence is characterized by glittering with different colors that change according to the angle from which the object is seen. It is due to the interference of light-waves reflected from the surfaces of very
thin multiple laminations, separated by equally thin or thinner layers of material possessing a contracting refractive index (Fox, 1953). Colors like those produced by soap bubbles and oil films on water are seen in the feathers of the barnyard cock (Gallus), starling (Sturnus vulgaris), and head of the male merganser (Mergus). The feathers of the peacock (Pavo cristatus) and of humming birds (Trochilidae) also show interference colors. The surfaces which produce these effects in some cases are attributed to the barbules (Mason, 1923) but others claim melanin granules are responsible for the phenomenon (Schmidt, 1952).

Blue is usually a structural color in birds. Commonly it is Tyndall scattering that produces blue coloring. Tyndall scattering refers to color produced when very small particles scatter the shorter waves in white light. This phenomenon is a cause of the blue color of the sky. The blue skin of the head and neck of the turkey (Meleagris gallopavo) and guinea fowl (Numida meleagris) are due to Tyndall scattering by protein particles. Melanin pigments behind the particles intensify the blue. The blue color in the feathers of the kingfisher (Halcyon), blue tit (Parus caeruleus), parrots, parakeets, and many other birds is due to Tyndall scattering by minute air-filled cavities within the keratin of the barbs. Purple is sometimes produced in feathers by the combined action of Tyndall blue over a background of reddish-brown pigment (Fox and Vevers, 1960).

Development and Differentiation of Feathers

The feather germ is an integrated developmental system consisting of three components of different embryonic origin: the epidermis of ectodermal origin, which gives rise to the keratinized feather; the dermal papilla, which produces the pulp; and melanoblasts of neural crest origin (Lillie and Wang, 1941). Following either natural molting or plucking, a new feather arises under the inductive influence of the dermal papilla at the bottom of the feather. The epidermal “collar”, surrounding the upper half of the papilla, is the formative center for the feather. On the dorsal surface of this cylindrical structure the rachis (or shaft) forms, and ridges which are destined to form the barbs arise in the ventral half; as they elongate by proliferation from below they become oriented tangentially, so that the base of each barb eventually is rooted in the rachis (Lillie and Juhn, 1932). Repeated mitotic divisions of the melanoblasts occur during this period of barb-cell elongation, and as the melanoblasts are transformed into melanocytes (in feathers or parts of feathers which are to be pigmented) pigment granules and melanosomes are either injected by melanocytes into barb cells (Strong, 1902) or blebed off and engulfed by the developing barb cell (Watterson, 1942). Feathers are pigmented first at the apical ends of the barbs and as keratinization and elongation proceed the pigmentation progresses toward the pulp and from apex to base of the feather.

As distal portions of the feather complete their growth, the sheath splits and the epidermal cylinder opens ventrally and unrolls into the familiar, flat, bilateral vane (for further details about this and other aspects of development in feathers, see Chap. 15, Lillie’s Development of the Chick (Hamilton, 1952)). The finished feather is a completely keratinized, non-living structure, but is attached at its base to the papilla which can repeat the entire process of forming a new feather under appropriate circumstances.

Genetic Contributions. Although the melanoblasts of all birds have much in common, as in the way they migrate and respond to developmental processes, it is obvious that there are different phenotypic expressions among the species and breeds.

Most information relating to genetic determination of color and pattern comes from studies of domestic fowl (Gallus). It has been well established by a variety of grafting techniques that melanocytes in-
variably produce in host feathers the specific color, color pattern, or lack of color which is characteristic of the donor breed (Willier and Rawles, 1940; Rawles, 1948). Even grafts of melanogenic skin of American robin (Turdus migratorius) tissue to White Leghorn chicken embryos produced robin-color in feathers of the host; the pigment was produced by donor (robin) melanoblasts which had migrated from the grafted tissue into the developing host feather germs (Rawles, 1939).

There is considerable variability in genetically-determined reactivity of birds to hormones; a few examples will serve to illustrate this fact (see Willier, 1942). In Brown Leghorn chickens the feather germ of either male or female can react to female steroids but not to male steroids. On the other hand, the Sebright bantam maintains a henny-type plumage in both sexes in the presence of either male or female hormones; gonadectomy of both males and females leads to the formation of cock-type plumage (Roxas, 1926). A third type is found in Reeves pheasant (Syrmaticus reevesi) in which feather follicles genetically male and those genetically female react differently to male and female hormones; gonadectomy of both males and females leads to the formation of cock-type plumage (Roxas, 1926). A third type is found in Reeves pheasant (Syrmaticus reevesi) in which feather follicles genetically male and those genetically female react differently to male and female hormones; gonadectomy of both males and females leads to the formation of cock-type plumage (Roxas, 1926). A third type is found in Reeves pheasant (Syrmaticus reevesi) in which feather follicles genetically male and those genetically female react differently to male and female hormones; gonadectomy of both males and females leads to the formation of cock-type plumage (Roxas, 1926). A third type is found in Reeves pheasant (Syrmaticus reevesi) in which feather follicles genetically male and those genetically female react differently to male and female hormones; gonadectomy of both males and females leads to the formation of cock-type plumage (Roxas, 1926). A third type is found in Reeves pheasant (Syrmaticus reevesi) in which feather follicles genetically male and those genetically female react differently to male and female hormones; gonadectomy of both males and females leads to the formation of cock-type plumage (Roxas, 1926). A third type is found in Reeves pheasant (Syrmaticus reevesi) in which feather follicles genetically male and those genetically female react differently to male and female hormones; gonadectomy of both males and females leads to the formation of cock-type plumage (Roxas, 1926).
pattern of males (Juhn and Gustavson, 1930), despite the fact that it causes explants to differentiate red melanoblasts (Hamilton, 1941) and blocks the expression of salmon pigmentation in both sexes of Silver Campine fowl (Nickerson, 1946b). In the laughing gull (Larus atricilla) testosterone causes black head feathering and red coloring of the beak, features that are characteristic of both sexes in breeding season (Noble and Wurm, 1940). The male black-headed gull (Larus ridibundus) fails to change its head feathers from white to dark brown following castration (Van Oordt and Junge, 1933).

Sex hormones also can influence the deposition of carotenoids. In both sexes of the starling the beak is colored black by melanin out of breeding season, but is a bright orange-yellow color due to carotenoid during breeding season. Castration produces black beaks in both sexes, which are changed to yellow by injection of androgens but not of estrogens (Witschi, 1961).

Thyroxine decreases the amount of black pigment deposited in the English sparrow (Miller, 1935), changes the pattern of feathers in Guinea fowl (Numida meleagris) (Hardesty, 1935), and increases the dark pigment in Brown Leghorn fowl (Juhn and Barnes, 1931; Blivaiss, 1947). In all cases concomitant structural changes are caused by thyroxine. Thyroidectomy of Brown Leghorn roosters is followed by replacement of the normal black, brown, red, and yellow melamins by a light reddish-brown pigment. The rate of growth of feathers and degree of barbulation also are decreased (Blivaiss, 1947).

The effects of pituitary hormones have been found, in almost all cases, to be mediated secondarily through gonads (Van Oordt and Junge, 1933; Hill and Parkes, 1935; Noble and Wurm, 1940) or, in a few instances, through thyroids (Miller, 1935; Parkes and Selye, 1937). The first indication that hormones of the pituitary gland could extra-gonadally affect the pigmentation of feathers came from the studies by Witschi (1936) on African weaver birds (Euplectes). He found that castrated males continued to undergo plumage changes, alternating bright and dull plumage in the manner seen in the intact bird (Witschi, 1935). Furthermore, the black pigmentation characteristic of males in nuptial plumage could be produced in normal or castrated birds (in basic plumage) of either sex by intramuscular injections of beef pituitary extracts. Further studies of pituitary extracts, including that of the turkey, revealed that several species of the so-called weaver birds (E. franciscanus, E. afer* Quelea quelea, Stegana paradisaea**) following plucking, would deposit dark pigment in response to their injection (Witschi, 1937, 1940).

Fractionation and purification of extracts showed that it was the luteinizing hormone (LH) activity which had the greatest potency in causing melanin pigmentation (Witschi, 1940). Human chorionic gonadotropin (HCG) (Segal, 1957) and PMS gonadotropin (Witschi, 1940), both of which have LH activity, gave positive responses. Follicle-stimulating hormone (FSH) was effective but only at very high levels (Segal, 1957). Whereas LH increased the activity of tyrosinase (accompanying pigmentation) in regenerating feathers of S. paradisaea, FSH, melanocyte-stimulating hormone (MSH), and adrenocorticotropic hormone (ACTH) did not (Hall and Okazaki, 1966). Thus, this response of weavers is rather specific and has been used as an assay for LH (ICSH) (Witschi, 1940; Segal, 1957; Thapliyal and Saxena, 1961). This assay is also reported to be very sensitive, detecting as little as 5 μg of LH. However, Ortman (1967) in a comparative study of three species of weavers failed to confirm the levels of sensitivity claimed by Witschi and found responsiveness to be variable.

* Witschi used afra as the species name, but the gender is wrong and is correctly afer.
** This bird does not weave a nest but is in fact a brood parasite; it is in the subfamily Viduinae of the family Ploceidae, whereas Euplectes and Quelea are in the subfamily Ploceinae.
Pigment is deposited in feathers within 12-24 hr after injection of a threshold amount of LH in *S. paradisaea*, but not until 30-54 hr after in *E. afer*. In either case the pigment appears well after the exogenous hormone would have been removed from circulation. LH induced a transient proliferation of melanocytes, generally not lasting more than 24 hr. PMS, on the other hand, caused melanization to persist for at least 72 hr in *S. paradisaea* and for 96 hr in *E. afer* (Ralph, Grinwich, and Hall, 1967a).

The mode of action of these agents in causing melanization of feathers remains to be discovered. Their effects are not mediated by way of the gonads, as noted above (see also Thapliyal and Saxena, 1961). In fact, estrogenic (but not androgenic) hormones inhibit the inductive action of gonadotropins on feathers in weavers (Witschi, 1936). However, very extensive attempts to demonstrate a local or direct action of LH upon regenerating feathers in two species of African finches (*E. afer* and *S. paradisaea*) failed completely (Hall, Ralph, and Grinwich, 1965). Additionally, LH does not appear to act via the hypothalamus, adrenal, thyroid, or pineal (Ralph, Grinwich, and Hall, 1967b).

**Seasonal Color Change.** Many birds show no obvious seasonal change of colors of adult plumage. In others a semblance of seasonal change is secondarily established without involving a molt and replacement of feathers; by wear or fading, the feathers change their appearance (Witschi, 1961; Smith, 1965). Melanin pigments seem to give feathers mechanical strength; pale portions of feathers abrade away, leaving dark portions little affected, thus making the bird appear darker (Parkes, K. C., personal communication). In some instances the beak or iris will show a seasonal difference in color.

Humphrey and Parkes (1959) have classified the patterns of succession of adult plumage in terms of number of molts and plumage types per cycle as follows:

1. One molt and one plumage per cycle. The length of the cycle is generally a year and there are three common variations of the basic plumage of the two sexes: (a) males and females wear dull basic plumage at all times (e.g., wrens, *Thryothorus* and *Troglydites*), (b) the male wears bright basic plumage and the female a dull one rather like that of the juvenile (e.g., red-winged blackbird, *Agelaius phoeniceus*), or (c) both sexes wear a bright basic plumage quite different in appearance from that of the juvenile bird (e.g., emperor goose, *Anser canagica*; European robin, *Erithacus rubecula*).

2. Male with two molts and plumages per cycle, female with one. Certain male weaver birds (*Pyromelana, Euplectes, Quetae*) are considered by Witschi (1935, 1936) to have two plumages and molts per cycle while the females have only one, but Humphrey and Parkes (1959) suggest that this needs more study.

3. One complete and one partial molt per cycle in both sexes. This is a very common pattern. The complete molt varies in temporal position and duration; the partial molt varies in extent as well as in position and duration. The latter may involve only a few feathers or nearly all of them and it is generally the body feathers that are most affected. In some species the female may change relatively little but in others she will be decidedly "brighter" than is either sex in the basic plumage. In many others the alternate plumage of both sexes is strikingly different from the basic plumage (e.g., Podicipedidae, Alcidae). On the other hand, both the alternate and basic plumes in both sexes are "dull" and practically identical in several species of birds (e.g., some waterfowl).

4. Two complete molts per cycle. Very few species are known to have two complete molts per cycle. This condition is found in the sharp-tailed sparrow (*Ammospiza caudacuta*), which shows little sexual and seasonal dimorphism, and the bobolink, the male wearing a bright alternate plumage which is replaced by a basic plumage like that of the female; the basic
and alternate plumages of the female are almost identical.

(5) Three molts and three plumages per cycle. A few species have a third molt and supplement or add specialized plumage. This is the case for the male of the ruff (Philomachus pugnax) and some species of ptarmigan (Tetraonidae).

Humphrey and Parkes (1959) believe that the plumages of most birds probably were not originally sexually, seasonally, or developmentally dimorphic (or polymorphic) but were dull or subdued in color and pattern. Species considered "primitive" have but one molt and one plumage per year. The bright plumages are considered as "added" when acquired by partial molts or "special" where molts occur only in the male.

Since the plumage comprises approximately 10% of the total weight of the bird, replacement of the plumage requires a considerable expenditure of energy. Primitively this expense probably was budgeted over a long period of time, and still tends to be in certain non-migratory birds of tropical latitudes, such as parrots. For the majority of modern birds, however, selection pressures associated with migration, reproduction, regulation of temperature, or development may have made it necessary that many feathers be replaced in a short period of time (Humphrey and Parkes, 1959). Such pressures appear to have been responsible for the great variety of morphology, color, and pattern in plumages of birds.

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