Coloration of Bird Plumage

Robert W. Ricci

Birds are our most colorful of animals. Not only do birds incorporate many of the ways that nature provides for creating color, but they do so in a dynamic, evolving manner based on sex, age, and season of the year. During the course of a year a Massachusetts birder can expect to find well over a thousand different forms of plumage to sort through in identifying a bird. The purpose of this article is to provide the reader with a survey of the three color-producing processes – pigments, light scattering, and light interference – found to be important in birds and to show that the multifarious colors and appearances arise from a relatively simple pattern of development.

Light, Color, and Pigments

Our primary source of white light comes from the sun. White light is actually a mixture of colored lights which are revealed when white light passes through a prism. Water droplets in the atmosphere can act as prisms and are the source of the many colors seen in the rainbow. But what is light, and how is it related to the individual colors that we see as part of the surface properties of bird plumage?

Visible light as a source of energy is best considered as a particle, called a photon. As a photon it can interact directly on a one-to-one basis with individual molecules. Molecules called dyes or pigments can give color to objects that contain them. How these colors come about is illustrated in Figure 1. For illustration purposes, we will think of white light as a mixture of red, orange, yellow, green, and blue light. In this example, all but the red light is absorbed by the surface pigment molecules, and the red light reflects off the surface. We therefore perceive the surface as red. In this way the color of an object depends upon which components of the white light are lost to the pigment molecules. Of course, if the surface reflects all components it will appear white, and if the surface molecules absorb all components it will appear black.

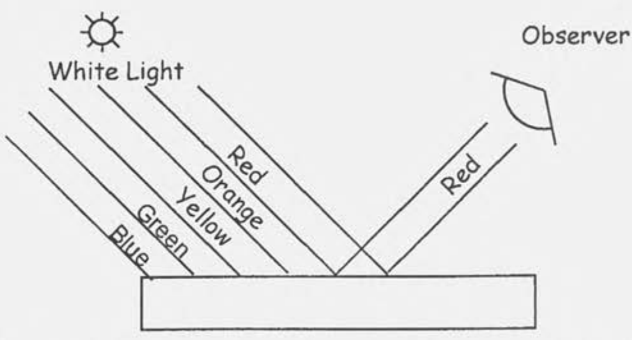

Figure 1. White light (seen as a composite of red, orange, yellow, green, and red lights) strikes a surface covered with a pigment capable of absorbing all the light components but red. The red light is reflected toward the observer.

Plumage Pigments

The typical feather structure is illustrated in Figure 2. The rachis is the central stem of the feather. Barbs come out of the rachis, and to these are attached the barbules. Most of the surface area of the feather is found on the barbules, and this is where the color resides. Pigment coloration is an important feature of bird plumage, and in this section we will discuss some of the important pigments found in birds.

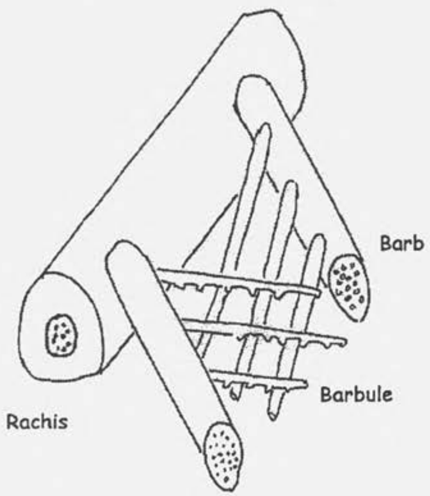

Figure 2. A bird feather, illustrating the rachis, barb, and barbules.

Blacks, Browns, and Grays. The most common pigments found in bird feathers are from the melanin family of chemical compounds that give rise to the black, brown, gray, and related colors. The melanin is synthesized in special cells called melanocytes, and then it is transported to the feather cells through tiny tubes or dendrites. In most cases, the melanin appears in the form of very small granules that are randomly distributed in the feather cells of the barbules. This arrangement gives rise to the deep velvet black seen, for example, in the American Crow.

Yellows, Oranges, and Reds. The bright yellows and reds found in birds are due almost exclusively to the presence of the carotenoid family of compounds. Unlike the melanins, birds are incapable of synthesizing their own carotenoids and depend on their diet to obtain them. One of the most common yellow carotenoids found in birds is lutein, which is widely distributed not only in feathers but also in bills, egg yolk, and the skin of the bird's feet. Lutein is probably most familiar to most New England birders as the yellow pigment seen in fall foliage. The pigment is always present in leaves, but its color is masked during the spring and summer by the green pigment chlorophyll. Lutein is ingested directly by foraging ducks, geese, and other plant eaters. Herbivorous insects, such as caterpillars, consume lutein and store it in their bodies, thus making it available to insect-eating birds such as warblers. Most insect eggs, small crustaceans, snails, and frogs are other sources of carotenoids.

Some ingested carotenoids are chemically altered by the bird's metabolism before being assimilated in the feather structure. A common example is the red pigment, canthaxanthin, which is found in a wide variety of birds from cardinals to flamingos. The widespread availability of carotenoids in nature normally assures that birds will not lack the materials needed to maintain their expected coloration. Under unnatural conditions, such as captivity, however, unexpected color changes can occur unless an effort is made to duplicate the bird's normal diet.

The respiratory pigment hemoglobin is a source of red color in the exposed skin areas of some birds. The head of the adult Turkey Vulture, the Wild Turkey's wattle, and the red patch on the head of the Sandhill Crane are three examples that birders will recognize.

Greens, Blues, and Whites. Green, blue, and white pigment in animals is rare, and I do not believe they are found in any birds typically found in this area. If we are to discover the source of these colors in local birds, therefore, we must first look at the wave nature of light.

Light and Structural Colors

Visible light as a radiating entity is best thought of as a wave characterized by a wavelength, as illustrated in Figure 3. The distance between successive crests or troughs determines the wavelength, and it is the difference in wavelength that characterizes the different colors of a light source. Visible light with the longest wavelengths is perceived as red, and as we scan through the spectral colors of orange, yellow, green, and blue, the wavelength decreases, with blue having the shortest wavelength in the visible range. The wave nature of light plays an important role in light scattering and light interference, two important methods of color development in bird plumage, and they will be discussed next.

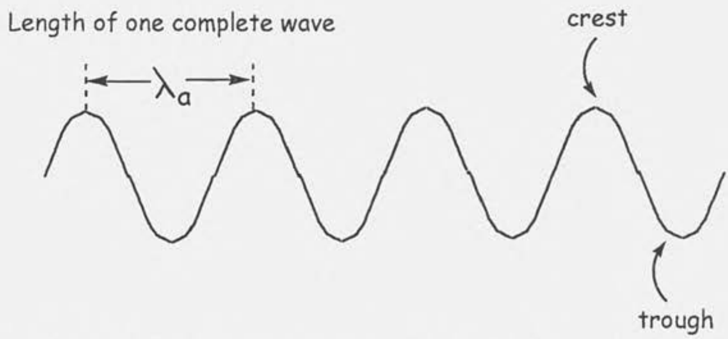

Figure 3. Light seen as a wave propagating through space. The light is characterized by a wavelength represented by the distance between successive crests.

Light Scattering

All surfaces, even those of transparent substances such as ice or glass, are capable of reflecting or scattering light. This is evident, for example, from the fact that we can see images reflected from the surface of a window pane. Increasing the surface area of an object will result in increased scattering of light. An icicle is clear and colorless, but snow is opaque and white, although they are both created from frozen water. The difference in appearance is due entirely to the enormous increase in surface area resulting from dispersing the ice in the form of tiny snow flakes. If the ambient light is white, such as sunlight, then the scattering will give the snow the appearance of being white. Notice that the change in appearance arises not because of a change in the chemical makeup of the material, but solely due to its structure, i.e., solid icicle versus tiny snow flakes. For this reason, scientists refer to this type of coloring as a "structural color."

A typical white feather is composed of barbules that are made up of a transparent solid protein called keratin. This material is filled with tiny air-filled cells, giving it a sponge-like appearance. These air-filled cells increase the total interior surface area of the barbules and effectively scatter the sunlight as it passes through. (It is for this reason that our own hair appears white in the absence of melanin.) The vast majority of white-winged creatures owe their coloration to the existence of these air-filled cells. Many flowers also owe their white color to the same phenomenon. For example, the white flowers of the petunia contain air-filled cells that scatter the sunlight to give them their brilliant white coloration. The cellular structure of flowers is delicate and can be easily crushed between your fingers. Squeezing a petal from a white petunia will destroy the air-filled cells, causing the petal to lose its coloration and become transparent. The cellular structure of a white feather is more resilient than that of a petal, but can be crushed by a few blows from a hammer, resulting in the loss of its white coloration also.

Tyndall Light Scattering

In the case of the white feather, the air-filled cells that scatter the light into a diffuse white glow are longer and wider than the wavelength of visible light. In that case all of the wavelengths are scattered back to our eyes, resulting in our perception of white. However, if the size of an air-filled cell is smaller than the wavelength of visible light, then there is a different interaction between the visible light and the cells. In this situation the air-filled cells do not scatter all the frequencies of light equally, but scatter the shorter wavelength components more. Thus we find that blue light is scattered most. Green light is also scattered, but much less so, and yellow, orange, and red are scattered the least. This type of light scattering will result in the light reaching our eyes being mostly blue. The effect can be quite dramatic, as in the Blue Jay, Indigo Bunting, and other birds with blue feathers. In each case the barbules contain air-filled cells that are smaller than the wavelength of visible light. The presence of similar-sized cavities is also responsible for the Scaup's pale blue bill and the powder-blue bill of the breeding male Ruddy Duck.

Wavelength-dependent scattering is also called Tyndall light scattering, after the British scientist John Tyndall, known for his research on the blue color of the sky. Sky blue is also due to light scattering; however, in this case the sunlight scatters from tiny solid dust-like particles suspended in the atmosphere.

In a similar way, the light, grayish-blue color of the Great Blue Heron is partly due to light scattering. The heron's downy underfeathers are fragile and in time disintegrate into dust-like particles that become trapped in the outer flight feathers. The dust particles then act as scattering centers, giving the light reflected from its feathers a bluish cast.

On my desk is a test tube filled with alcohol in which I have placed a Blue Jay feather. The feather has lost its blue color and has turned as black as the Jay's necklace. The liquid has diffused into the feather structure and filled the cells with alcohol. The alcohol molecules are – in an optical sense – similar to the molecules that make up the horny material of the feather, and as a consequence the cells have "disappeared" as far as the white light is concerned. If I were to remove the feather from the alcohol and allow it to dry, it would turn blue again.

Now, filling the cells with alcohol explains why the blue disappeared, but does not explain why the feather turned black. It turned black because, just below the light-scattering region of the feather, there is a layer of melanin-filled cells that absorb the light. This layer also plays an important role in the intensity of the blue shade of the feather because it acts as an absorber of all the radiation that is *not* scattered by the scattering layer. If the melanin in the bottom layer of the Jay's feather is removed with a bleaching agent such as hydrogen peroxide, the blue pales considerably as white light now reflected from the bottom layer mixes with the scattered blue light. Painting the back surface with black paint would restore the deep blue color.

In many cases, the light-scattering feather surfaces contain a third top layer of transparent cells that can acquire a yellowish appearance through the presence of a blue-absorbing pigment. This is the case with many green-plumaged birds, where the color is a result of the combination of yellow outer layer, a Tyndall light-scattering middle layer, and a bottom, melanin-filled, light-absorbing lower layer. The yellow outer layer acts as a light filter, both absorbing some of the blue component of the

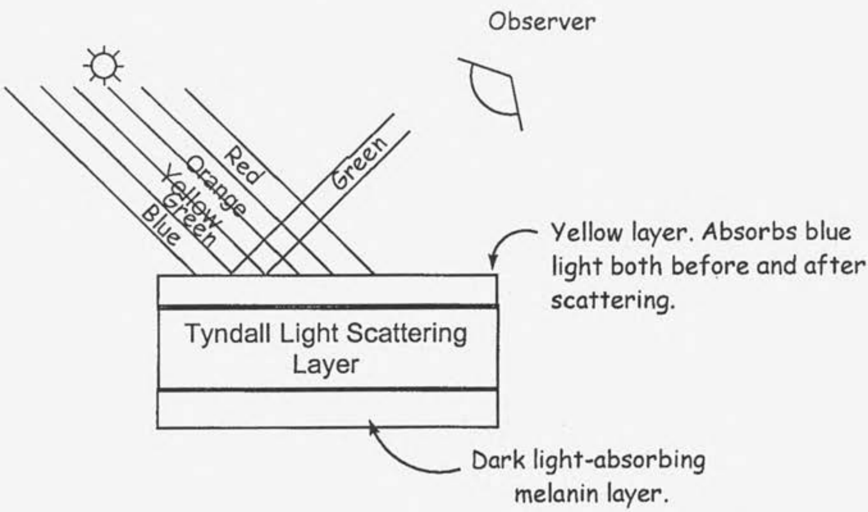

Figure 4. How green plumage is created. A top yellow layer acts as a filter for the blue component of white light, and it also absorbs the scattered blue light. Bottom melanin layer absorbs all light not scattered (mostly red, orange and yellow). Only the scattered green light emerges from the feather surface.

entering white light before it reaches the Tyndall layer and most of the remaining blue light scattered out of the Tyndall layer. The green component of the light from the scattering layer is unaffected by the blue-absorbing pigment, and this light emerges from the feather to provide the green hue. Again, any light not scattered by the middle layer or scattered downward by the middle layer is removed through absorption into the melanin-filled lower layer. This coloring process is illustrated in Figure 4. With some birds, the top layer of cells acquires a reddish translucent quality that results in purple-colored plumage.

Each of the three layers are subject to genetic variation, and this enables bird breeders to produce blue, white, and yellow-plumaged birds from green-plumaged stock, as is seen, for example, with domesticated parakeets. Breeding birds that have little or no yellow pigment in their top layer will eventually result in offspring that are blue. By selecting for a lot of pigment in the top layer, breeders can produce the yellow variety; breeding for transparent outer layers, white-light-scattering middle layer, and loss of melanin backing will result in light blue and white parakeets.

Iridescence

Iridescent colors represent the third manner that nature employs to adorn our avian friends.

Iridescent colors are intense, simmering, and change with angle of view. More than fifty Massachusetts' species display iridescence. The green speculum of marsh ducks, the bronze plumage of Wild Turkeys, and the glimmering green and purple coloration of starlings in winter are a few notable examples.

To understand how iridescence arises, we must first look at a third property of light called wave interference. Visible lights coming from two light sources are capable of interacting with each other (see Figure 5). In one case, when the two light waves interact, the crest of one wave overlaps the crest of the second wave, and trough meets trough, resulting in a combined wave that is more intense than the two original beams. This process is called constructive interference and results in the

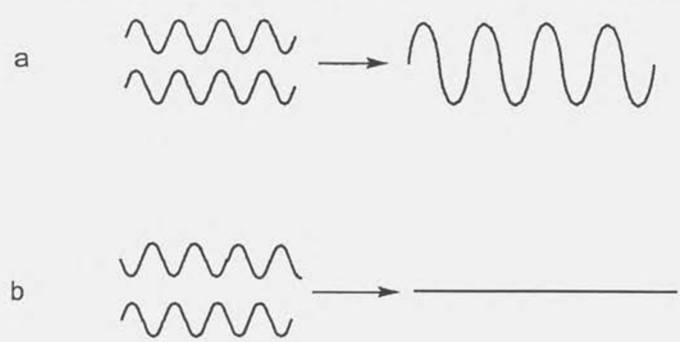

Figure 5. (a) Constructive interference of two waves. (b) Destructive interference of two waves.

reinforcement of the light intensity. In the second case, when the two waves interact, the crest of one wave overlaps the trough of the second, resulting in a much less intense beam than either of the two individual beams. In this case the two waves cancel each other out in a process called destructive interference.

Iridescence arises due to the interaction between light waves and the structure of the material through which the light is passing. It is another example of a structural color. Some species of birds are equipped with genes that precisely control the arrangement of a translucent melanin-like material in the feather cells. For example, the material may be deposited in the form of tubes. Each tube in the feather cell is of the same size, arranged side by side in neat layers, with the same spacing between layers, and looking for all the world like the "supermarket shelf" stacking of canned goods. In other species the tubes are replaced by an orderly arrangement of thin, flat, rigid plates, giving the appearance of a tiled floor. It is these orderly cellular structures that give rise to the iridescent colors found in birds.

Hummingbirds have flat barbules, and the iridescent cells in the barbules are stacked together like shingles on a house. The cells consist of ultrathin layers of translucent air-filled plates. The plates are all of the same thickness and form a series of layers. Sunlight enters the plates, and some light is reflected back out from each surface of each layer toward the observer. These reflected beams of sunlight act as secondary light sources capable of interfering with each other. For light of a particular color, the extra distance traveled between layers will be equivalent to its wavelength, and this color will be reinforced through constructive interference. The effect will be amplified at each layer, giving rise to an intense burst of color.

This process is illustrated in Figure 6. Green is the most typical iridescent color, but other colors are found. In general, thicker optical layers give rise to yellows (brassy colors) and reds, and thinner layers to violet and blues.

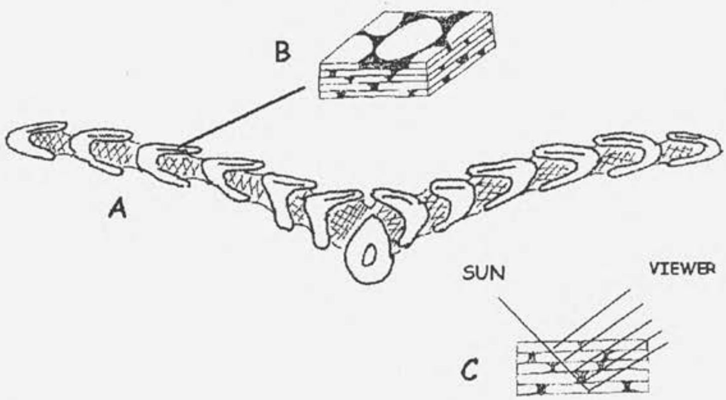

Figure 6. The structure of a hummingbird wing. A. Cross sectional view of a hummingbird barb and two attached barbules. B. An expanded view of the plate structure of the barbule cells. C. Illustration of how sunlight reflects from each surface of the plates, resulting in constructive interference for light of the correct wavelength (color).

Sources

Durrer, H. 1984. Colouration. In *Biology of the Integument*, 239-247, New York: Springer-Verlag.

Farrant, P. A. 1997. *Color in Nature: A Visual and Scientific Exploration*. New York: Sterling Publishing Co, Inc.

Fox, D. L. 1979. *Biochromy: Natural Coloration of Living Things*. Berkeley: University of California Press.

Greenwaldt, C. H., Werner, B., Friell, D. D. 1960. "The Iridescent Colors of Hummingbird Feathers." *Proceedings of the American Philosophical Society*, Vol. 104, No. 3.

Nassau, K. 1983. *The Physics and Chemistry of Color*. New York: John Wiley & Sons.

Simons, H. 1971 *The Splendor of Iridescence*. New York: Dodd, Mead & Co.

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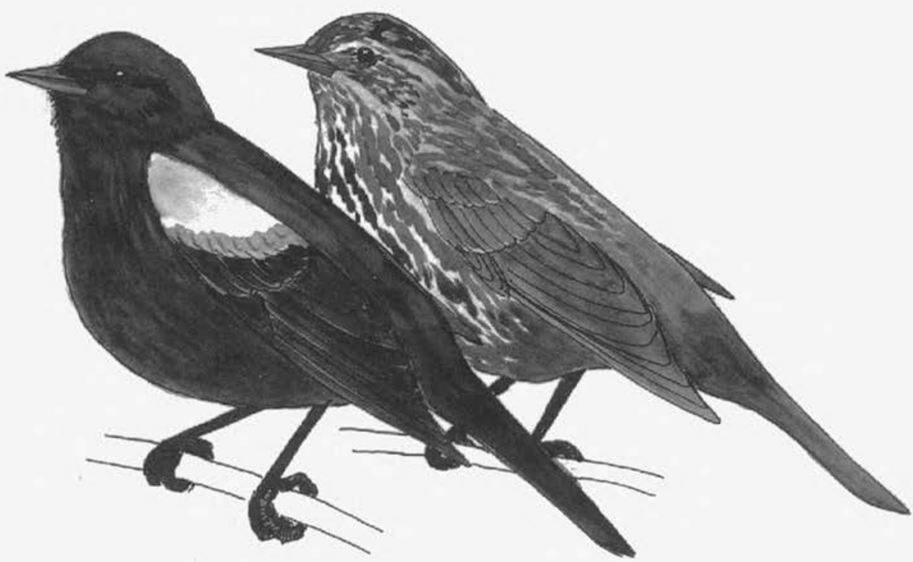

RED-WINGED BLACKBIRD, GEORGE C WEST