# What Birds

*Evolution has endowed birds with a system of color vision that surpasses that of all mammals, including humans*

# See

By Timothy H. Goldsmith

MARTIN HARVEY *Peter Arnold, Inc.*



We humans customarily assume that our visual system sits atop a pinnacle of evolutionary success. It enables us to appreciate space in three dimensions, to detect objects from a distance and to move about safely. We are exquisitely able to recognize other individuals and to read their emotions from mere glimpses of their faces. In fact, we are such visual animals that we have difficulty imagining the sensory worlds of creatures whose capacities extend to other realms—a night-hunting bat, for example, that finds small insects by listening to the echoes of its own high-pitched call.

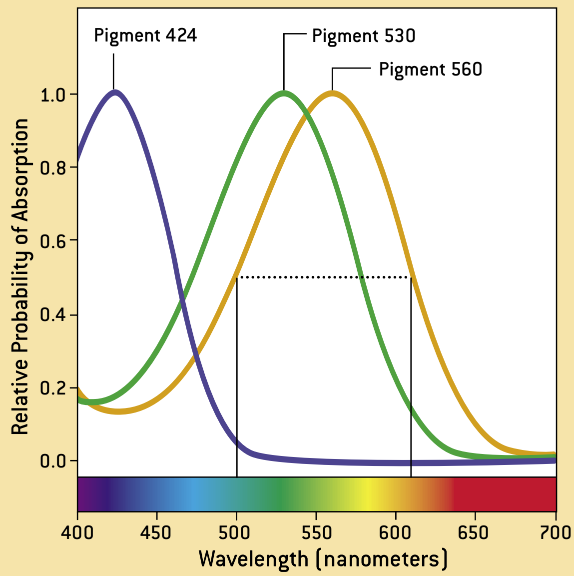
Our knowledge of color vision is, quite naturally, based primarily on what

AFRICAN GROUND HORNBILL (*Bucorvus leadbeateri*), like all birds, sees the world in a rich tapestry of color that we can scarcely imagine. Birds have this capacity because they have retained color-processing cone cells in the eye that mammals lost millions of years ago.

# Human Color Vision

Humans and some other primates see the colors that they do as a result of interactions among three types of cone cells in the retina of the eye. Each cone type contains a different pigment that is sensitive to a given range of wavelengths of light. The three types of cones are maximally sensitive at about 560, 530 and 424 nanometers.

The two thin vertical lines in the graph rise from wavelengths that are absorbed equally by pigment 560. Even though photons from rays with a wavelength of 500 nanometers (*in the blue-green*) have more energy than photons from rays having a wavelength of 610 nanometers (*in the orange*), both cause the same response of the pigment and thus cause the same excitation of the cone cell. A single cone cell therefore cannot reveal to the brain the wavelength of the absorbed light. To distinguish one wavelength from another, the brain must compare signals from cones with different visual pigments.




humans see: researchers can easily perform experiments on cooperative human subjects to discover, say, what mixtures of colors look the same or different. Although scientists have obtained supporting information from a variety of other species by recording the firing of neurons, we remained unaware until the early 1970s that many vertebrates, mostly animals other than mammals, see colors in a part of the spectrum that is invisible to humans: the near ultraviolet.

The discovery of ultraviolet vision began with studies of insects—and with the curiosity of a remarkable Englishman, Sir John Lubbock, Lord Avebury. Friend and neighbor of Charles Darwin, member of Parliament, banker, archaeologist and naturalist, Lubbock discovered sometime before 1882 that in the presence of UV light, ants would pick up their pupae and carry them to dark areas or to areas illuminated by longer wavelengths of light. Then, starting in the mid-1900s, Austrian naturalist Karl von Frisch and his students (and their students) showed that bees and ants not only see UV light as a distinct color but use ultraviolet in skylight as part of a celestial compass.

The finding that a great many insects perceive UV light led briefly to the idea that this spectral region provides a private sensory channel that avian predators cannot see. Nothing, however, could have been further from the truth. Work of the past 35 years has shown that birds, lizards, turtles and many fish have UV receptors in their retinas. Why, then, are mammals so different? What caused them to have impoverished color vision? The search for answers has turned up a fascinating evolutionary story and led to fresh insights into the extraordinarily rich visual world of birds.

## Overview/*An Evolutionary Tale*

- Color vision of vertebrates depends on cone cells in the retina. It turns out that birds, as well as lizards, turtles and many fish, have four types of cone cells, whereas most mammals have only two types.
- The progenitors of mammals had the full complement of cones, but during a period in their evolution when they were mainly nocturnal—and thus color vision was not crucial to their survival—early mammals lost two types of cone cells.
- The ancestors of a group of Old World primates, which includes humans, "reclaimed" a third cone by means of mutation of one of the existing cones.
- Most mammals, however, still have only two cones, making mammalian color vision—even that of humans and their kin—distinctly limited when compared with the visual world of birds.

## How Color Vision Evolved

THE DISCOVERIES are best understood if one first knows some basic details of how any organism perceives color. First, a common misconception must be put to rest. It is true, as many youngsters learn in school, that objects absorb some wavelengths of light and reflect the rest and that the colors we perceive "in" objects relate to the wavelengths of the reflected light. But color is not actually a property of light or of objects that reflect light. It is a sensation that arises within the brain.

Color vision in vertebrates begins with the cone cells in the retina, the layer of nerve cells that transmits visual signals to the brain. Each cone contains a pigment that consists of some variant of the protein opsin, linked to a small molecule called retinal, closely related to vitamin A. When the pigment absorbs light (or, more precisely, absorbs discrete packets of energy called photons), the added energy causes the retinal to

JEN CHRISTIANSEN; SOURCE: TIMOTHY H. GOLDSMITH change shape, triggering a cascade of molecular events leading to excitation of the cone cell. This excitation in turn leads to activation of retinal neurons, one set of which fires impulses in the optic nerve, conveying information to the brain about the light received.

The more intense a light, the more photons are absorbed by the visual pigments, the greater the excitation of each cone, and the brighter the light appears. But the information conveyed by a single cone is limited: by itself, the cell cannot tell the brain which wavelength of light caused its excitation. Some wavelengths are absorbed better than others, and each visual pigment is characterized by a spectrum that describes how absorption varies with wavelength. A visual pigment may absorb two wavelengths equally, but even though their photons contain different energies, the cone cannot tell them apart, because they both cause the retinal to change shape and thus trigger the same molecular cascade leading to excitation. All a cone can do is count the photons it absorbs; it cannot distinguish one wavelength from another. Hence, a cone can be equally excited by an intense light at a relatively poorly absorbed wavelength and by a dim light at a readily absorbed wavelength.

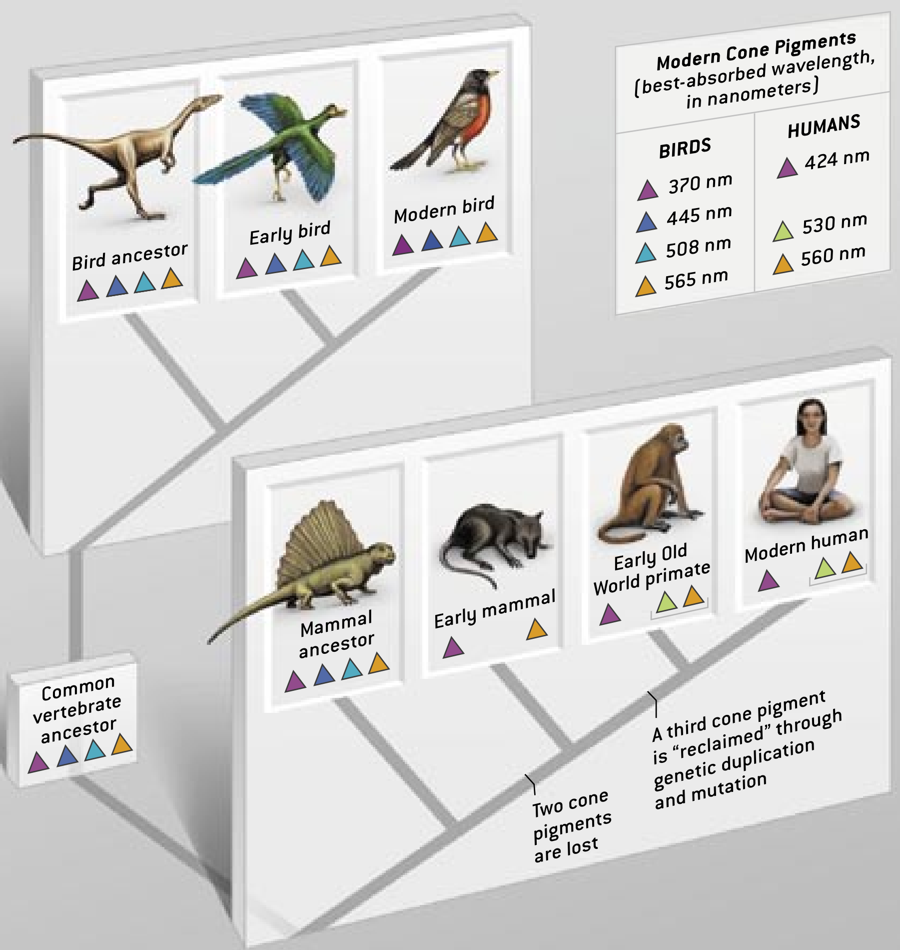
The important conclusion to draw here is that for the brain to see color, it must compare the responses of two or more classes of cones containing different visual pigments. The presence of more than two types of cones in the retina allows an even greater capacity to see different colors.

The opsins that distinguish one cone from another have provided a way to study the evolution of color vision. Researchers can figure out the evolutionary relations of opsins in the various classes of cones and from different species by examining the sequences of nucleotide bases (or DNA "letters") in the genes that code for these proteins. The resulting evolutionary trees reveal that opsins are ancient proteins that existed before the emergence of the predominant groups of animals that populate the earth today. We can trace four lineages of vertebrate cone pigments, named descriptively after the spectral region in which they are most sensitive: long-wavelength, mid-wavelength, short-wavelength and ultraviolet. All major groups of vertebrates have rods in the retina as well as cones. The rods, which contain the visual pigment rhodopsin, provide vision in very dim light. Rhodopsin is similar in both structure and absorption characteristics to the cone pigments most sensitive to

## THE AVIAN ADVANTAGE

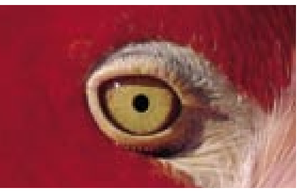
By analyzing the DNA of contemporary species, scientists have been able to look back in time and determine how cone pigments have changed as vertebrates have evolved. The work indicates that very early vertebrates had four cone types (*colored triangles*), each containing a different pigment. Mammals lost two of these cones during their early evolution, very likely because these animals were nocturnal and cones are not needed for vision in dim light. Birds and most reptiles, in contrast, retained four spectrally different cone pigments.

After the dinosaurs died out, mammals began to diversify, and the lineage that gave rise to the Old World primates of today—African monkeys, apes and humans—"reclaimed" a third cone through duplication and subsequent mutation of the gene for one of the remaining pigments. Because humans evolved from this primate lineage, we are unlike most of our fellow mammals in having three cones (instead of two) and trichromatic color vision—an improvement, but nothing to challenge the more nuanced visual world of birds.




JEN CHRISTIANSEN; SOURCE: TIMOTHY H. GOLDSMITH wavelengths in the middle of the visual spectrum, and it evolved from those pigments hundreds of millions of years ago.

Birds have four spectrally distinct cone pigments, one drawn from each of the four evolutionary lineages. Mammals, however, typically have only two cone pigments, one maximally sensitive in the violet and the other sensitive at long wavelengths. The likely explanation for this paucity is that during their early evolution in the Mesozoic (245 million to 65 million years ago), mammals were small, secretive and nocturnal. As their eyes evolved to take advantage of the night, they became increasingly dependent on the high sensitivity of rods and less dependent on color vision. Consequently, they lost two of the four cone pigments that their ancestors once possessed—pigments that persist in most reptiles and birds.


Flamingo

COLOR is not actually a property of light or of objects that reflect light. It is a sensation that ARISES WITHIN THE BRAIN.

The demise of the dinosaurs 65 million years ago presented mammals with new opportunities for specialization, and they began to diversify. One group—among which were the progenitors of humans and the other Old World primates living today—took up a diurnal life, spread out into the trees, and made fruit an important part of their diet. The colors of flowers and fruits frequently contrast with the surrounding foliage, but mammals, with only one long-wavelength-sensitive cone pigment, would have been unable to see contrasting colors in the green, yellow and red regions of the spectrum. A solution for these primates, though, was present in the evolutionary toolbox.

Occasionally in the cell divisions that occur during the formation of eggs and sperm, an unequal exchange of parts of chromosomes leads to production of a gamete that possesses a chromosome containing extra copies of one or more genes. If subsequent generations maintain these extra genes, natural selection may preserve useful mutations that arise in them. As Jeremy Nathans and David Hogness, working at Stanford University, have shown, something of this kind occurred during the past 40 million years in the visual system of our ancestral Old World primates. The unequal exchange of DNA in a reproductive cell and subsequent mutation of an extra copy of a gene for a pigment sensitive to long wavelengths resulted in the creation of a second long-wavelength-sensitive pigment, which had a shift in its wavelength of maximum sensitivity. This primate lineage thus differs from that of other mammals in having three cone pigments instead of two and trichromatic color vision.

Though a significant improvement, this system does not equip us with the quintessence of color vision. Ours is still the result of an evolutionary reclamation job and remains one pigment short of the tetrachromatic visual system found in birds and in many reptiles and fish. Our genetic heritage also handicaps some of us in another way. Both our genes for long-wavelength-sensitive pigments lie on the X chromosome. Because males possess only one X chromosome, mutations in either of the pigment genes can leave the affected male with a diminished capacity to distinguish between reds and greens. Females suffer from this kind of color blindness less often, because if a pigment gene is damaged on one copy of the X chromosome they can still make the pigment under the guidance of the healthy gene on their other copy of X.

Cone pigments are not the only elements that were lost from the retina during the early evolution of mammals. Each cone of a bird or reptile contains a colored oil droplet; these droplets no longer exist in mammalian cones. The droplets, which contain high concentrations of molecules called carotenoids, are placed so that light passes through them just before reaching the stack of membranes in the outer segment of the cone where the visual pigment is located. The oil droplets function as filters, removing short wavelengths and narrowing the absorption spectra of the visual pigments. This reduces the spectral overlap between pigments and increases the number of colors that, in principle, a bird can discern.


THE AUTHOR

*TIMOTHY H. GOLDSMITH* is professor emeritus of molecular, cellular and developmental biology at Yale University and a fellow of the American Academy of Arts and Sciences. He has studied vision of crustaceans, insects and birds during a span of five decades. He also nurtures an interest in the evolution of human cognition and behavior and has enjoyed thinking and writing with legal scholars in association with the Gruter Institute for Law and Behavioral Research. For a dozen years before retiring, Goldsmith taught a science course for students in the humanities and social sciences and, with William Zimmerman, wrote the text *Biology, Evolution, and Human Nature.*


## Testing Color Vision in Birds

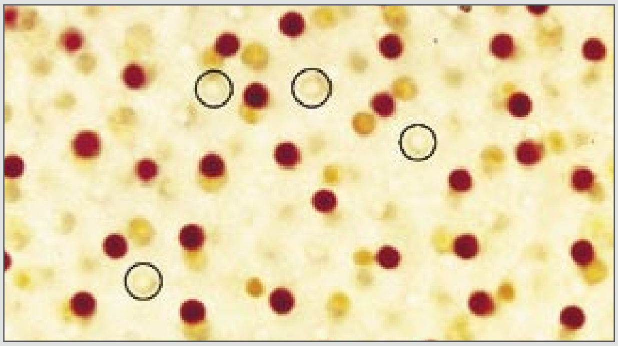
THE PRESENCE of four types of cones containing different visual pigments certainly implies that birds have color vision. Yet a direct demonstration of the ability to see colors requires behavioral experiments in which birds show that they can discriminate colored objects. These experiments must also eliminate other cues, such as brightness, that the birds might be using. Although researchers have performed experiments of this type on birds, they began examining the role of UV cones only in the past couple of decades. My former student Byron K. Butler and I decided to use the technique of color

BORIS ROESSLER *DPA/Corbis*

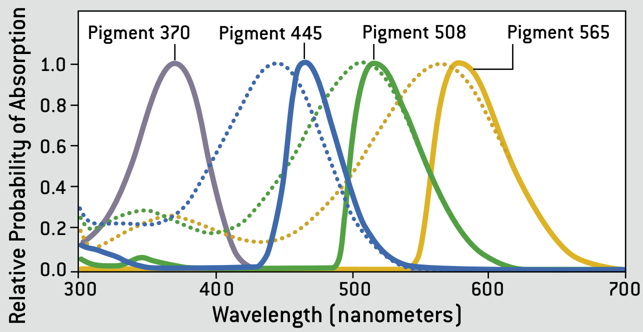
## THE IMPORTANCE OF CONE OIL DROPLETS

Cones of birds and many other vertebrates have preserved several features lost from the cones of mammals. The most important of these for color vision is oil droplets. The cones of birds contain red, yellow, nearly colorless and transparent droplets. A micrograph of a chickadee retina (*left*) clearly reveals the yellow and red droplets; black rings mark several colorless droplets. All but the truly transparent droplets act as filters that remove light having short wavelengths.

The filtering effect narrows the spectral sensitivity of three of the four cones of birds and shifts it to longer wavelengths (*graph*). By restricting the wavelengths to which the cones respond, the droplets enable the birds to distinguish more colors than they would see distinctively without the droplets. Ozone in the upper atmosphere absorbs wavelengths shorter than 300 nanometers; therefore, ultraviolet vision for birds involves only the near ultraviolet: the wavelength band from 300 to 400 nanometers.



**FILTERING EFFECT OF DROPLETS**




matching to explore how the four cones participate in vision.

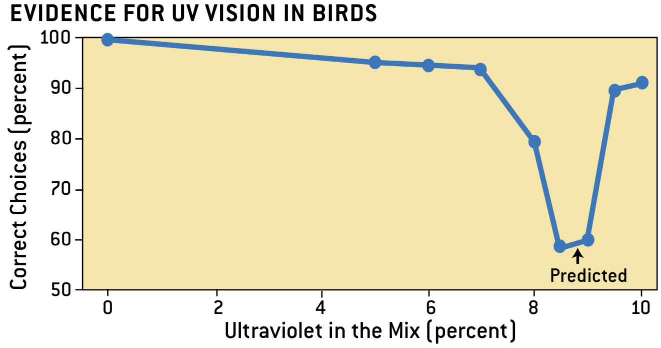
To grasp how color matching works, first consider our own color vision. A yellow light excites both types of long-wavelength cones in humans. Furthermore, it is possible to find a mixture of red and green lights that excites the same two cones to exactly the same extent, and this mixture will be perceived by a viewer as the same yellow seen when the pure yellow light is presented. In other words, two physically different lights may match in color—a reminder that the perception of color is produced in the brain. Our brains discriminate colors in this region of the spectrum by comparing the outputs of the two long-wavelength cones.

Armed with knowledge of the physical properties of the four cones and the oil droplets, Butler and I were able to calculate what mixture of red and green wavelengths birds should see as having the same hue as a particular yellow wavelength. Because human and avian visual pigments are not identical, this mixture was different from what we would predict for humans asked to make the same color match. If the birds responded to the lights as we predicted, that result would confirm our measurements of visual pigments and oil droplets and would allow us to go on to explore whether and how the ultraviolet-sensitive cones are involved in color vision.

We used as subjects small Australian parakeets called budgerigars (*Melopsittacus undulatus*). We trained the birds to associate a food reward with a yellow light. A budgerigar sat on a perch from which it viewed a pair of lights about three feet away. One was the yellow training light, the other a variable mixture of red and green. During testing, a bird flew to the light where it anticipated food. If it went to the yellow, a small seed hopper opened briefly, and the bird got a quick snack. If it went to the wrong light, it got no reward. We changed the mixture of red and green in an irregular sequence, as well as varying the positions of the two lights so the birds were unable to associate food with either the right or left side. We also changed the intensity of the training light so the birds would be unable to use brightness as a cue.

At most mixtures of red and green, the birds were readily able to select the yellow training light and get their reward of seed. But when the mixture contained about 90 percent red and 10 percent green—a proportion we calculated would match the yellow hue of the training light—the birds became confused, and their choices became erratic.

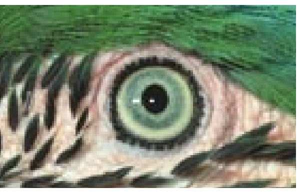
**EVIDENCE FOR UV VISION IN BIRDS**




DO BIRDS REALLY SEE UV WAVELENGTHS as distinct colors? In an experiment, the author and his colleagues showed that they do. The researchers trained parakeets to distinguish a violet training light from light made up of mixtures of blue and UV. When the mixture had only about 8 percent UV, it matched the hue of the training light and the birds made many errors. Their choices fell to chance at the point (*arrow*) where the author had calculated—on the basis of measurements of the visual pigments and oil droplets in bird cones—that the colors would match.

TIMOTHY H. GOLDSMITH (*micrograph*); JEN CHRISTIANSEN; SOURCE: TIMOTHY H. GOLDSMITH (*illustrations*)

Reassured that we could predict when birds would see color matches, we sought similar evidence to show that UV cones are contributing to tetrachromatic color vision. In this experiment we trained the birds to receive food at a violet light and explored their ability to distinguish this wavelength from mixtures of blue and a broad band of wavelengths in the near UV. We found that the birds could clearly distinguish the violet light from most mixtures. Their choices fell to chance, however, at 92 percent blue and 8 percent UV, the proportions we calculated would make the hue of the mixture indistinguishable from the violet training light. This result means that UV wavelengths are seen as distinct colors by birds and that UV cones participate in a tetrachromatic visual system.


Macaw

**Scientists were unaware until the 1970s that many animals see colors in THE NEAR ULTRAVIOLET.**

## Beyond Human Perception

OUR EXPERIMENTS provided evidence that birds use all four cones in their color vision. But it is difficult—impossible, in fact—for humans to know what their perception of colors is actually like. They not only see in the near ultraviolet, but they also can see colors that we cannot even envision. As an analogy, we might say that our trichromatic color vision can be represented in a triangle, whereas their tetrachromatic color vision requires an additional dimension, giving a tetrahedron or triangular pyramid. The space above the floor of the tetrahedron encompasses a variety of colors that lie beyond direct human experience.

How might birds make use of this wealth of color information? In many species of birds, males are much more brightly colored than females, and following the discovery of UV sensitivity, researchers sought evidence that UV colors not visible to humans might influence mate choice.

In one line of research, Muir Eaton, then at the University of Minnesota, studied 139 species of birds in which the sexes look the same to a human observer. Based on measurements of wavelengths of light reflected from the plumage, he deduced that in more than 90 percent of these species, the eye of a bird sees differences between males and females that ornithologists had not previously recognized.

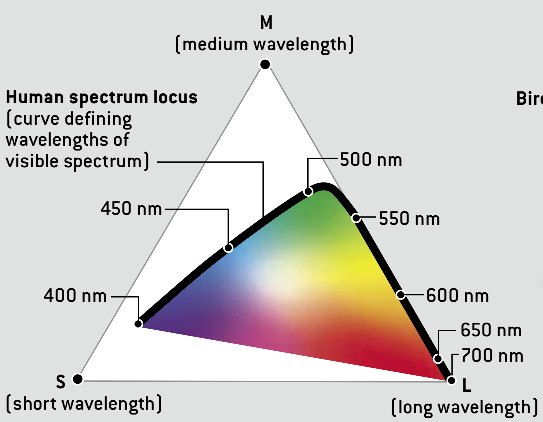
In a study of males from 108 species of Australian birds, Franziska Hausmann and an international group of col-

### A VIRTUAL PEEK INTO THE VISUAL WORLD OF BIRDS

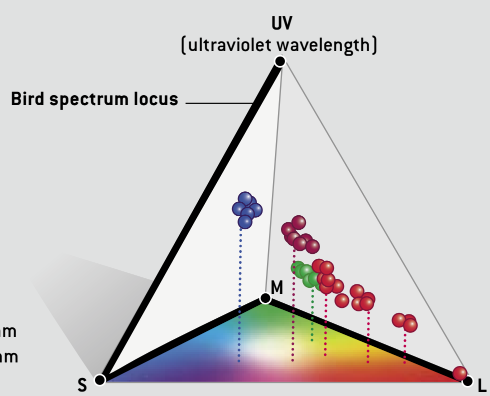
The color vision of humans can be mapped as a triangle. All the colors of the spectrum that we humans can see plot along the heavy black curve lying inside the triangle, and all the many other colors that are made by mixtures of lights lie below the curve.

To map the color vision of a bird, we need to add another dimension, and the result is a solid, a tetrahedron. All the colors that do not activate the UV receptor lie in the floor of the tetrahedron; however, because the cone oil droplets increase the number of colors a bird can see [*as explained in top box on preceding page*], the spectrum locus follows the edges of the triangular floor rather than the shark fin shape of the human color triangle. The colors that involve the UV receptor fall in the space above the floor. For example, the red, green and blue plumage of the painted bunting (*photograph*) reflects varying amounts of UV light in addition to the colors that we humans see (*graph*).

To indicate graphically the colors that the female bunting sees when she looks at her mate, we have to move from the plane of the triangle to the three-dimensional volume of the tetrahedron.



HUMAN VISION



BIRD VISION


MALE PAINTED BUNTING

MARTIN HARVEY *Corbis* (*top photograph*); ARTHUR MORRIS *Corbis* (*bottom photograph*); JEN CHRISTIANSEN; SOURCE: TIMOTHY H. GOLDSMITH (*illustrations*)

## Imagining a UV World

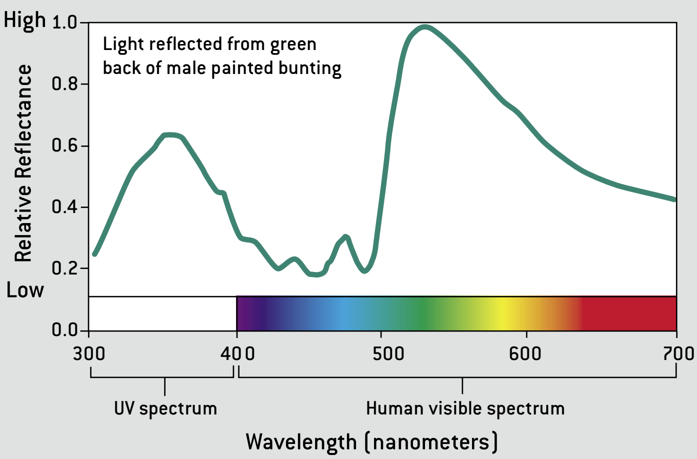
Although no one knows what the world looks like to birds, these images of black-eyed Susans offer a glimpse of how an ability to see ultraviolet light might change the way the world looks. To us, the center of the flower is a small dark disk (*left*). But a camera equipped to detect only ultraviolet light "sees" patterns invisible to us, including a much larger dark ring (*right*). These photographs were made by Andrew Davidhazy, a professor of imaging and photographic technology at the Rochester Institute of Technology. —*The Editors*

leagues found colors with a UV component significantly more often in plumage that is involved in courtship displays than in feathers from elsewhere on the birds. Furthermore, groups in England, Sweden and France have studied the blue tit (*Parus caeruleus*), a Eurasian near relative of chickadees of North America, and starlings (*Sturnus vulgaris*), with results indicating that females are in fact attracted to those males that show the brightest UV reflectance. Why should this matter? UV reflectance from the plumage of birds depends on the submicroscopic structure of feathers, so it can serve as a useful indicator of the health of male birds. Amber Keyser and Geoffrey Hill of the University of Georgia and Auburn University have shown that male blue grosbeaks (*Guiraca caerulea*) with the most, brightest and most-UV-shifted blue in their plumage are larger, hold the most extensive territories with abundant prey, and feed their offspring more frequently than other males do.

More generally, having a UV receptor may give an animal an advantage in foraging for food. Dietrich Burkhardt of the University of Regensburg in Germany has shown that the waxy surfaces of many fruits and berries reflect UV light that might advertise their presence. Jussi Viitala of the University of Jyväskylä in Finland and colleagues have found that small falcons called kestrels are able to locate the trails of voles visually. These small rodents lay scent trails of urine and feces that are reported to reflect UV light, making them visible to the UV receptors of kestrels, particularly in the spring before the scent marks are covered by vegetation.

People unaware of these intriguing findings often ask me, "What does ultraviolet vision *do* for birds?" The question seems to imply that sensitivity to UV must be a peculiarity or even a feature that self-respecting birds should be able to live happily without. We are so locked into the world of our own senses that, although we readily understand and fear a loss of vision, we cannot conjure a picture of a visual world beyond our own. It is humbling to realize that evolutionary perfection is a will-o'-the-wisp and that the world is not quite what we imagine it to be when we measure it through a lens of human self-importance. SA

The colors reflected from small regions of feathers are represented by clusters of points: bright red for the breast and throat, darker red for the rump, green for the back, and blue for the head. (We cannot, of course, show the colors the bird sees, because no human can perceive those colors.) The more ultraviolet in the color, the higher the points are above the floor. There is a distribution of points within each of the clusters because the wavelengths of reflected light vary within the regions, such as what we humans see as the red areas of the breast and throat.




### MORE TO EXPLORE

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**Ultraviolet Signals in Birds Are Special.** Franziska Hausmann, Kathryn E. Arnold, N. Justin Marshall and Ian P. F. Owens in *Proceedings of the Royal Society B,* Vol. 270, No. 1510, pages 61–67; January 7, 2003.

**Color Vision of the Budgerigar (Melopsittacus undulatus): Hue Matches, Tetrachromacy, and Intensity Discrimination.** Timothy H. Goldsmith and Byron K. Butler in *Journal of Comparative Physiology A,* Vol. 191, No. 10, pages 933–951; October 2005.