Understanding Avian Vision: The Key to Using Light in Bird Management

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Abstract: Vision is a primary and highly developed sensory pathway in birds. Light, both diffuse and wavelength-specific (e.g., as produced by lasers) has recently been demonstrated as a potential means of effecting changes in timing and consistency of flock response to an approaching vehicle (simulating an aircraft) and as an avian dispersal method. However, in experiments to date, the effectiveness of light in eliciting an avoidance or dispersal response in birds has varied by species and context. To effectively use light in managing avian conflicts with humans, a better understanding of the complexities of avian retinal physiology relative to phototaxic responses to the environment is necessary. My objectives are to provide an overview of research pertaining to 1) anatomical features of the avian eye and 2) the ecological implications of retinal wavelength sensitivity, and 3) discuss the application of light for resolving avian conflicts with humans. I also suggest that future evaluations of light-based management methods for birds should include integration of aposematic colors and color pattern treatments for seeds and in combination with chemical repellents, as well as quantification of the effects of light wavelength, pulse frequency, and beam configurations of lasers, and aircraft-mounted light in eliciting avian dispersal and avoidance behavior.

Key Words: avian eye, avoidance behavior, damage management, dispersal, laser, light, vision, wavelength

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INTRODUCTION

Society has enjoyed both the beauty and benefits of birds (e.g., as pollinators) and marveled at their adaptations to exploit extreme habitats (e.g., maintenance of water balance while foraging at sea) and temporal resources (e.g., migration). However, modern society contends with the challenges of habitat and species conservation, while facing increasing conflicts with birds in agriculture, as competitors for sport and commercial fisheries, predators of livestock and aquaculture stocks, amplifying hosts and vectors of disease, sources of property destruction, and as threats to aircraft movements. Moreover, the combination of responsibilities to conserve threatened or endangered species and protect fragile habitats while maintaining food production, commerce, and leisure is further complicated by progressive restriction of wildlife management options toward use of non-lethal methods (Dolbeer 1998; Smith et al. 1999; Blackwell et al. 2000, 2002). However, several authors have noted that non-lethal technologies (e.g., auditory, chemical, physical, and visual) are few, and that those available are often limited in effectiveness by circumstance (Mason and Clark 1992, Clark 1998, Dolbeer 1998). The ever-present need to reduce conflicts between birds and humans, and the complexities of social and political tendencies influencing wildlife management underscore the need to identify methods that can broaden the base of effective avian repellents and the circumstances governing their application (Blackwell et al. 2002).

A common factor in non-lethal technologies, including foraging repellents, is a reliance on visual recognition of the treatment (e.g., consumption of a secondary repellent and the associated learned avoidance; see Clark 1998, Dolbeer et al. 1998, Blackwell et al. 1999). Avian vision represents a primary sensory pathway and is, subsequently, highly developed. Sillman (1973) noted that the importance of vision to birds is evident in the relative size of the eyes to the skull area (in some species the combined weight of the eyes exceeds that of the brain), and that no treatment of the biology of birds is sufficient without consideration of vision. However, to effectively use light in managing avian conflicts with humans, a better understanding of the complexities of avian retinal physiology relative to phototaxic responses to the environment is necessary. My objectives are to provide an overview of research pertaining to 1) anatomical features of the avian eye and 2) the ecological implications of retinal wavelength sensitivity, and 3) discuss the application of light for resolving avian conflicts with humans.

ANATOMICAL FEATURES OF THE AVIAN EYE

Given the breadth of habitats and niches occupied by birds, there is an associated wide variation in visual capabilities among species. Here, I will direct my discussion of the anatomy and functional aspects of the avian eye topically as potentially important to the use of light in managing pest birds. Unless otherwise cited, I refer to and follow Sillman's (1973) review of work relating to the functional anatomy and physiology of the avian eye.

Refractive Apparatus and Accommodation

The avian eye has three characteristic shapes: a) flat, representing the majority of birds; b) globular,

common to most Falconiformes; and c) tubular, found in most owls (Strigiformes) and some eagles (Accipitridae) (Walls 1942). Species that have a greater need for visual acuity (e.g., some Passeriformes and most Falconiformes) have eyes in which the ratio of the vertical and horizontal axes more closely approaches unity, thus producing a globular shape. The effect of the near unity in axes is that the size of the image cast on to the retina will be larger if the axial length of the eye is greater (i.e., increasing visual acuity). Walls (1942) suggested that animals traveling at great speed (e.g., Falconiformes) have increased visual acuity to detect movement and avoid collision. In contrast, owls, which are either nocturnal or crepuscular, depend not on increased visual acuity as much as increased sensitivity.

As with most terrestrial vertebrates, the major structure of refraction in the avian eye is the cornea. Refraction is the change in direction of propagation of a light wave when it passes from one medium to another in which the wave velocity is different. Here, the greatest change in the index of refraction occurs as light passes from the air through the eye. The lens, though playing a role in refraction, serves mainly as a fine adjustment during accommodation. Accommodation is the alteration of the refractive apparatus to maintain focus as the distance to an object changes. In birds the cornea generally plays the primary role in accommodation. However, for diving birds the lens is likely the major organ of accommodation, because the index of refraction within the cornea is similar to that of water. Thus, depending upon species ecology and the medium (habitat) occupied by the species, sensitivity and functional aspects of maintaining focus on an object can differ. In addition, how light information is processed, via the retina, can differ among species.

Retinal Organization

Because of its cellular organization, many of the complex functions of the avian visual system are accomplished in the retina (as opposed to the higher centers of the nervous system). The retina first senses light, integrates the information, and passes the information onto the brain in the form of nerve impulses. Other structures of the eye serve only to present the image to the retina. Also, as in most animals, the avian retina is duplex in nature, containing both rods (responsible for dim light or scotopic vision) and cones (responsible for acute, bright light or photopic vision). The cones also serve to mediate color vision. The outer segments of the rods and cones contain the visual pigments, photosensitive material responsible for the absorption of light striking the visual cells (see reviews by Dartnall 1962, Sillman 1973). For an animal to have the ability to distinguish wavelengths (i.e., hue) irrespective of brightness, it must have a minimum of two separate classes of photoreceptor with different, but overlapping spectral sensitivities (see below; Bowmaker 1987). Thus, most diurnal birds have retinas that are dominated by cones, with the rods being few in number and located primarily in the periphery.

In addition to single cones, the avian retina also possesses double cones (described in all classes of vertebrates, except placental mammals). For example, the retinae of most diurnal birds are represented by a single class of rods, a single class of longwave-sensitive double cones, and four classes of single cone (Bowmaker et al. 1997; Hart et al. 1998, 2000). Also, each of the cone classes is associated with a particular type of oil droplet, and the oil droplets are highly refractile lipid-based globules situated at the distal end of the inner segments of cone photoreceptors (Sillman 1973, Goldsmith et al. 1984, Hart et al. 1998). Because cones are oriented such that their outer segments are farthest from incoming light, the light reaching the photosensitive outer segment of the retina will have to pass through the oil droplet (Bowmaker 1987). Most oil droplets contain carotenoid pigments (Wald and Zussman 1937, Goldsmith et al. 1984), which alter the spectral transmission characteristics of the oil droplets and act as long-pass "cut-off" filters (i.e., they may transmit longer wavelengths, but at a specific wavelength absorb shorter wavelengths and effectively cut off all short-wave light; Bowmaker 1977; Chen et al. 1984; Bowmaker 1987; Partridge 1989; see also Maier and Bowmaker 1993; Hart et al. 1998, 2000). The spectral sensitivity of a cone photoreceptor is determined both by the spectral transmission of the oil droplet (and that of other ocular media, including lens and cornea) and the spectral absorbance of the visual pigment (Hart et al. 1998).

Spectrophotometric and electrophysiological studies of the avian retina suggest that birds can distinguish colors ranging from the ultraviolet (~325–400 nm; >30 species; see Bennett and Cuthill 1994) to the red (>700 nm; Huth and Burkhardt 1972, Bowmaker 1987, Bennett and Cuthill 1994), spanning the range visible to humans (400–700 nm). However, Hart et al. (1998, 2000) noted that a physiological dichotomy in short-wavelength photoreception might exist and be dependent upon phylogeny. For example, in addition to cone visual pigments maximally sensitive in the long-wave, medium-wave, and short-wave regions of the human-visible spectrum, avian retinae contain single cones with a visual pigment maximally sensitive to either violet (e.g., mallard *Anas platyrhynchos*, Jane and Bowmaker 1988; Humbolt penguin *Spheniscus hmuboldti*, Bowmaker and Martin 1985; European starling *Sturnus vulgaris*, Hart et al. 1998) or ultraviolet (e.g., European starling *Sturnus vulgaris*, Hart et al. 1998; red-billed leiothrix *Leiothrix lutea*, Maier and Bowmaker 1993; rock dove *Columba livia*, Kreithen and Eisner 1978; Bowmaker et al. 1997).

Finger and Burkhardt (1994) provided the following contrast between human and avian vision (see also Walls 1942, Bennett et al. 1994). Human color vision is based on three color channels, each originating at one of three different types of photoreceptor. Therefore, three primary color sensations (blue/green/red) are evident, each

resulting from stimulation of only one color channel. Secondary spectral colors in human color vision are mixtures of two neighboring primary colors (i.e., two of three receptors are stimulated) producing yellow (red and green) and cyan (blue and green). If the non-spectrally neighboring primary colors red and blue are mixed, purple is produced (a color not included in the spectrum of light produced by a prism or grating).

Birds, however, are considered tetrachromatic and, in some species, possibly pentachromatic. In tetrachromatic vision, four primary colors should be expected: ultraviolet (UV), blue, green, and red. Also, three spectrally neighbored mixed colors are possible: UV-blue, blue-green, and green-red. Further, there are three combinations of non-spectrally neighboring primary colors possible, causing non-spectral secondary colors: blue-red, UV-green, and UV-red. Stimulation of a combination of three of four color channels in birds is suspected to produce a new class of second-order mixed colors, ternary colors: UV-green-red, UV-blue-green, UV-blue-red, and blue-green-red. Finger and Burkhardt (1994) noted that plumages exhibiting the aforementioned colors, with the exception of green, generally contrast in brightness and spectral composition with background conditions (see *Signaling* below).

However, before considering specific implications of a light wavelength on the ecology of a species (e.g., plumage color and ambient light conditions), we must clarify the measure of intensity of a wavelength in terms of the animal's perception.

Perception

Vertebrates (as well as invertebrates and plant chloroplasts) respond directly to the number of photons (i.e., the photon flux) striking photoreceptors (Endler 1990, see also Endler and Thery 1996). Thus, the perceived brightness of a light or reflected light (e.g., a plumage color pattern) is dependent upon 1) light reflectance and transmission to the eye of the animal, 2) light transmission, refraction, and photoreception within the eye (species-specific), and 3) species-specific neural processes in the retina and brain that lead to the perception of light (Endler 1990). However, species-specific physiological differences can modify color perception. Specifically, spectral sensitivity as related to animal behavior can in some cases be differentiated from *color vision.* Goldsmith (1994) noted that the implications of wavelength dependent behaviors, activities driven by different spectral classes of receptors or different combinations of spectral classes of receptor do not generally reflect quantitatively the distribution of photoreceptors within the retina. Instead, they reflect a neural filtering where spectral cues are interpreted by the central nervous system in specific ways (e.g., peripherally, such as the use of polarized light by bees and ants). Goldsmith suggested, therefore, that the presence of more than one spectral class of receptor does not necessarily indicate that the animal is capable of dissociating chromatic cues from other features of the object.

Thus, as evidenced in the preceding discussion, avian species vary markedly in eye structure and physiology. Specific adaptations to maintaining focus, fixing upon an image (e.g., species-specific foveal structure; see Sillman 1973), light intensity, and wavelength perception serve to distinguish the niche occupied by each species.

ECOLOGICAL IMPLICATIONS OF RETINAL WAVELENGTH SENSITIVITY

Ultraviolet Vision

Response to various wavelengths of light (whether visually or peripherally perceived) raises a myriad of questions as to the ecological implications for a bird species. Arguably, these questions abound most in consideration of the ability of some avian species to perceive UV light (e.g., Maier 1993, Goldsmith 1994). Bennett and Cuthill (1994) reviewed evidence for UV vision in birds and the spectral properties of UV light, and discussed in detail hypotheses for the function of UV vision in birds and their plausibility. These hypotheses concern the role of UV vision in 1) orientation (Kreithen and Eisner 1978; Emmerton and Delius 1980; Parrish et al. 1981, 1984), 2) foraging (Avery et al. 1999; Hart et al. 1998, 2000), and 3) signaling (Maier 1993, Bennett et al. 1996). However, as noted earlier, wavelength perception (including UV) as related to any behavior, is influenced by ambient light and media through which the light passes; light passing through a medium is scattered by the molecules that it encounters.

Specifically, the scattering of light by particles in the air, particularly material that is small relative to the wavelength of the light (e.g., dust particles, oxygen, or nitrogen) is proportional to the inverse of the 4th power of the wavelength (Lythgoe 1979), termed the Rayleigh effect (Bennett and Cuthill 1994). Thus, UV light will be scattered more than light of longer wavelengths. At the short wavelength end of the human-visual spectrum similar effects occur, such that the sky appears blue to humans (see Lythgoe 1979). One effect of this wavelength-dependent scattering is that distant objects are likely to appear more indistinct in the UV. Still, another consequence is that UV and other short wave-lengths will be more susceptible to scattering from any imperfections in the animal's ocular media, termed chromatic aberration (Lythgoe 1979, Bennett and Cuthill 1994). Both effects tend to reduce the spatial resolution and contrast that animals perceive using UV wavelengths (particularly at distance).

Further, because the available light around dawn and dusk is proportionately higher in short wavelengths (i.e., long-wavelength light is scattered more during dawn and dusk; see also Lythgoe 1979, Endler 1993), animals active at these times are particularly likely to use UV wavelengths in activities such as foraging, mate choice, and orientation (Bennett and Cuthill 1994). However,

different site-specific concentrations of photosensitive cells within the retina of some avian species allow for simultaneous use of short- and long-wavelength light. For example, in their investigation of the coordinated roles of the European starling's visual pigments, oil droplets, and receptors relative to the photic environment, Hart et al. (1998) noted that the placement of longwavelength-sensitive (LWS) and UV-sensitive cells (UVS) is likely correlated with tasks such as scanning the celestial hemisphere for aerial predators (LWS) and ground foraging (UVS). Also, the diurnal Eurasian kestrel (*Falco tinnunculus*) and other raptors are suspected to key on scent-marked runways of small rodents; rodents mark these areas with urine and feces, which are visible in the UV (Viitala et al. 1995; see also Boonstra et al. 1996).

Signaling

Light also is integral in communication between conspecifics, predator avoidance, and resource selection. For example, because the conspicuousness of an animal towards conspecifics or predators is dependent upon both plumage or pelage characteristics and background and ambient light conditions, bird colors can, thus, be classified as cryptic, partly cryptic, or contrasting to the environment and thus have signal character (Endler 1990, Finger and Burkhardt 1994, Endler and Thery 1996). Signal colors seem to be adapted for producing maximal differences in stimulation of color channels in bird color vision (i.e., stimulating one, a pair, or a combination of the four types of photoreceptors; Finger and Burkhardt 1994; see also Vorobyev et al. 1998).

Birds also react to signal colors (e.g., aposematic or warning colors) from fruits and prey, either via learned responses or, possibly, innately. Some fruits from bird-dispersed plants, and potential insect prey, share self-advertising structures that incorporate color and patterning as cues to consumer organisms. The fitness of both the fruit and insect species depends upon appropriate visual signaling to ensure accurate identification by potential consumers or predators (Herrera 1985). Likewise, learned or innate response to warning patterns (e.g., black and yellow or black and red stripes) on potential vertebrate prey (e.g., coral snakes *Micrurus* spp. and *Leptomicrurus* spp., Smith 1975; the yellow-bellied sea snake *Pelamis platurus*, Caldwell and Rubinoff 1983; see also Lindström et al. 1999) serves not only to increase the fitness of the prey, but quite likely the predator as well. Given avian response to signal colors, there is potential for the integration of light-based techniques (i.e., via reflected colors or color patterns) with seed treatments, and primary or secondary repellents.

Navigation

In addition to signal properties, light is also considered integral to avian navigation, both directly and via photochemical reactions. For example, Munro et al. (1997) showed that under white (full spectrum) and green light (571 nm), juvenile Tasmanian silvereyes (*Zosterops l. lateralis*) oriented in the appropriate migratory direction, while they were disoriented under red (633 nm) light. These findings are comparable with previous work done with adult silvereyes (Wiltschko et al. 1993) and suggest that light-dependent processes are involved in an orientation mechanism used by both juvenile and adult migrants (i.e., the internal compass; see also Wiltschko and Wiltschko 1995, 1999). Deutschlander et al. (1999) suggested that behavioral and neurophysiological data for magnetic orientation in birds are indicative of a two-pigment mechanism mediated by short- to mid-wavelengths, and an antagonistic long-wavelength mechanism. The function of these wavelength dependent orientation mechanisms exemplifies the peripheral response to color noted above (see *Perception* above).

LIGHT AS A BIRD MANAGEMENT TOOL

The complexity of avian ecologies as related to light perception does not negate effective light-based damage management applications. For example, wildlife managers have reduced avian damage to crops by using light to attract European starlings and blackbirds (Icteridae) into traps (Meanly 1971). Further, light in the form of selected seed or bait color has also been investigated as a means of reducing avian crop depredation (Avery et al. 1999) and preventing consumption by birds of poisoned baits intended to control mammalian pests (Hartley et al. 1999). Further, a secondary foraging repellent, recently registered by the U.S. Environmental Protection Agency as a turf treatment (see Dolbeer et al. 1998; Blackwell et al. 1999), is purported to be a UV absorber (K. Ballinger, DCV Inc., Wilmington, DE, unpublished data), possibly appearing to birds as a dark area on turf.

In addition, researchers have also investigated light as a means of altering habitat around airports or alerting to birds the presence aircraft and dispersing them from the airspace. For example, van Tets et al. (1969) recommended that runway lighting exclude wavelengths < 530 nm to reduce attraction of insects and spiders and, subsequently, their avian and Chiropteran predators. Also, low- to moderate-power long-wavelength (633–650 nm) lasers (an acronym for Light Amplification by Stimulated Emission of Radiation) have recently been demonstrated as effective dispersal tools against some avian species (e.g., double-crested cormorants *Phalacrocorax auritus* [Glahn et al. 2001]; Canada geese *Branta canadensis* [Blackwell et al. 2002]), and represent a promising technology for bird control at airports (Blackwell et al. 2002). Specifically, Blackwell et al. (2002) described the behavior observed in Canada geese as a neophobic avoidance response to the approaching laser beam or beam spot contrasted against a dark background. However, response to laser treatment can vary within species (particularly in primarily diurnal birds; Blackwell et al. 2002), possibly due to the effect of artificial light sources in urban areas and the period

required for the bird to dark adapt (see pigment migration; Arey 1916, Walls 1942, Blough 1957, Adler and Dalland 1959).

In addition, aircraft-mounted light has been considered for nearly three decades as a possible means of increasing visibility of aircraft to birds (Lustick 1973, Larkin et al. 1975, Blokpoel 1976, Thorpe 1977, Briot 1986, see also Bruderer et al. 1999). Only recently, however, has the effect of vehicle-mounted light received formal research as to its efficacy in producing avian avoidance (see Blackwell et al. 2001). Blackwell et al. (2001) found that full spectrum 250-w landing lights pulsed alternately at 0.75 hertz influenced avian behavior in response to an on-coming vehicle, but avoidance behavior was not consistent. Future work will include evaluations of ecologically important wavelengths (see Belton 1976, Hart et al. 1998) and pulse frequencies. For example, Samson and Young (1973) showed that increasing contrast between a stimulus (i.e., flash intensity) and background results in increased peak-to-peak amplitude in flash-evoked response within the optic tectum of rock doves (*Columba livia*).

SUMMARY AND FUTURE

Though vision is a primary sensory pathway for birds, our understanding of species-specific ecological implications of wavelength perception and phototaxic behavior is limited. Moreover, methods to incorporate light in managing conflicts between birds and humans are few and cursory. However, advances in the use of light to manage problem birds have been made via investigations of seed and bait color preference, the application of laser technology for bird dispersal, and investigations for incorporating aircraft-mounted light to increase avian awareness of approaching aircraft. Future evaluations of light-based management methods for birds should include integration of color and color pattern treatments for seeds and in combination with chemical repellents, as well as quantification of the effects of light wavelength, pulse frequency, and beam configurations of lasers and aircraft-mounted light in effecting avian dispersal and avoidance behavior.

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